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Acritarch assemblages from the Oville and Barrios Formations, northern Spain: A pilot proposal of a middle Cambrian (Series 3) acritarch biozonation in northwestern Gondwana

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ABSTRACT

This paper presents a re-study of acritarchs from the Cambrian Oville and Barrios Formations in the Cantabrian Zone, northern Spain. The excellent preservation of the acritarchs, their great abundance and diversity, and good stratigraphic control of the sections examined allows one to establish a detailed middle Cambrian (Series 3) acritarch biozonation, and to consider their potential usefulness for global Cambrian chronostratigraphy. Six middle Cambrian (Series 3) zones (IMC1–IMC6), and one Furongian assemblage in the Barrios Formation are recognized. The IMC1–IMC5 zones, previously described in a preliminary manner (Palacios, 2008), are now characterized in detail, and a new IMC6 Zone is defined which is characterized by the first occurrence of *Stelliferidium magnum*, *Timofeevia phosphoritica* and *T. microretis*. The co-occurrence in the study area of acritarchs and trilobites makes it possible to correlate the two types of biozone. New species (*Comasphaeridium maximum* sp. nov., *Eliasum fombellae* sp. nov., *Timofeevia simplex* sp. nov. *Timofeevia heteromorpha* sp. nov., *Timofeevia densa* sp. nov., *Tubulosphaera craterae* sp. nov., and *Vulcanisphaera cantabrica* sp. nov.) are recognized, and the diagnoses of *Eliasum*, and *Symplassosphaeridium cambriense* are emended.

1. Introduction

The biostratigraphic zonation of the middle Cambrian in northern Gondwana is based mainly on trilobites. In Baltica and Avalonia, the major divisions are based on a succession of paradoxidid trilobites, with subdivisions mostly provided, where possible, by olenids and agnostids. In northern Gondwana the divisions are based mainly on a succession of paradoxidid and solenopleuridid trilobites (Liñán et al., 2002; Gozalo et al., 2003a). In the current Cambrian subdivisions, the middle Cambrian is equivalent to undefined Cambrian Series 3 (Peng et al., 2012). The base of Series 3 has not been defined, although the proposed limit (FAD of *Ovatoryctocara granulata* and of *Oryctocephalus indicus*) approximately coincides with the classic lower-middle Cambrian boundary, and the top is defined as the lower boundary of the Furongian Series.

Acritarchs, a polyphyletic assemblage of form taxa of planktic organic-walled cysts, provide a further means of determining Cambrian biochronology. They have proven to be a useful compliment to trilobites in correlation across Avalonia, Baltica, and northern Gondwana. Acritarchs generally can be extracted in great numbers from any fine-grained siliciclastic rock that was deposited under normal marine conditions. They provide a means for detailed sampling, and locally may provide the only fossil age constraints.

Middle Cambrian acritarch based zonations have been proposed by, among others, Vanguestaine and Van Looy (1983) for Gondwana, by Martin and Dean (1981, 1988) for Avalonia, and by Volkova (1990) and Volkova and Kiryanov (1995) for Baltica. Molyneux et al. (1996) establish a correlation between the acritarch zones of Baltica and Avalonia. Two problems have hampered the use of these biozones in middle Cambrian chronostratigraphy: (i) in Avalonia and Baltica, the Cambrian Series 3 stratigraphic record includes significant hiatuses (Mens et al., 1990; Landing, 1996; Palacios et al., 2009); and (ii) there are identification problems of some of the diagnostic acritarch species, e.g., *Cristallinium* and *Timofeevia* (Palacios et al., 2009, and this paper).

For this study area, Cramer and Díez de Cramer (1972) were the first to report data on acritarchs from the Oville Formation and the first zonation with acritarchs in the Cambrian of Spain was performed in this study area (Fombella, 1978, 1979). Nevertheless, the stratigraphic position of the samples and potential correlations with trilobite biozones were not presented in any detail in those studies. Palacios (2008) gave a preliminary review of the biostratigraphic data, establishing five biozones in the middle Cambrian which correlated with the previously established trilobite zones.

In the study area (Fig. 1), a detailed zonation of Middle Cambrian trilobites in the sections of Porma (Sdzuy, 1968, 1995; Gozalo et al., 2003b) and Barrios de Luna (Sdzuy, 1968; Liñán & Gozalo in Aramburu et al., 2006) have contributed to characterizing the Leonian, Caesaraugustian, and lower Languedocian regional stages. Palacios

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(2008) provided the first biostratigraphic data of acritarchs from the Porma and Barrios de Luna sections (detailed in this paper: Figs. 2, 3, 6, 7). The first systematic studies of acritarchs (Fombella, 1977, 1978, 1979) were based on material from the Oville Formation, but their chronostratigraphy (Fombella, 1979, 1986), aimed at spanning the middle Cambrian–Tremadoc, was confusing. The Tremadoc age assignment to the upper Oville Formation was based on an erroneous Tremadoc age identification of species (Fombella et al., 1993) in the Adrados section (Fombella, 1986). New data of acritarchs and trilobites (Fig. 5, Plate XVI, 5–7) in the Adrados Section (Figs. 2, 5) reported in this paper clearly indicate a middle Cambrian age.

2. Geological context

The areas dealt with in this study are located in the vicinities of the Rivers Luna and Porma in the northern and northeastern part of León Province in northern Spain (Fig. 1). In accordance with Lotze (1961) and Julivert (1971), the investigated areas are part of the south of the Cantabrian Zone in the Thrust Sheet and Fold Region, subdivided into a number of thrust nappe systems: the Somiedo-Correcillas Unit, the Sobia-Bodon Unit, and the Esla Unit (Fig. 1). The Somiedo-Correcillas Unit contains the closest to complete Cambrian successions. The stratigraphically lowest rocks are referred to the Narcea Group (Lotze, 1956; Pérez Estaun, 1978). This comprises greywacke and mudrocks formed by turbidite deposition, and consists of poor assemblages of organic-walled microfossils dominated by bacterial forms (Palacios and Vidal, 1992) considered Neoproterozoic. The contact with overlying Cambrian rocks is an erosive angular unconformity that is generally considered to be Cadomian. The basal Cambrian deposits belong to the Herrería Formation as described by Compte (1938), and include diverse lower Cambrian acritarchs (Palacios and Vidal, 1992), together with trilobites at the top (Lotze, 1961; Sdzuy, 1961) which is included in the

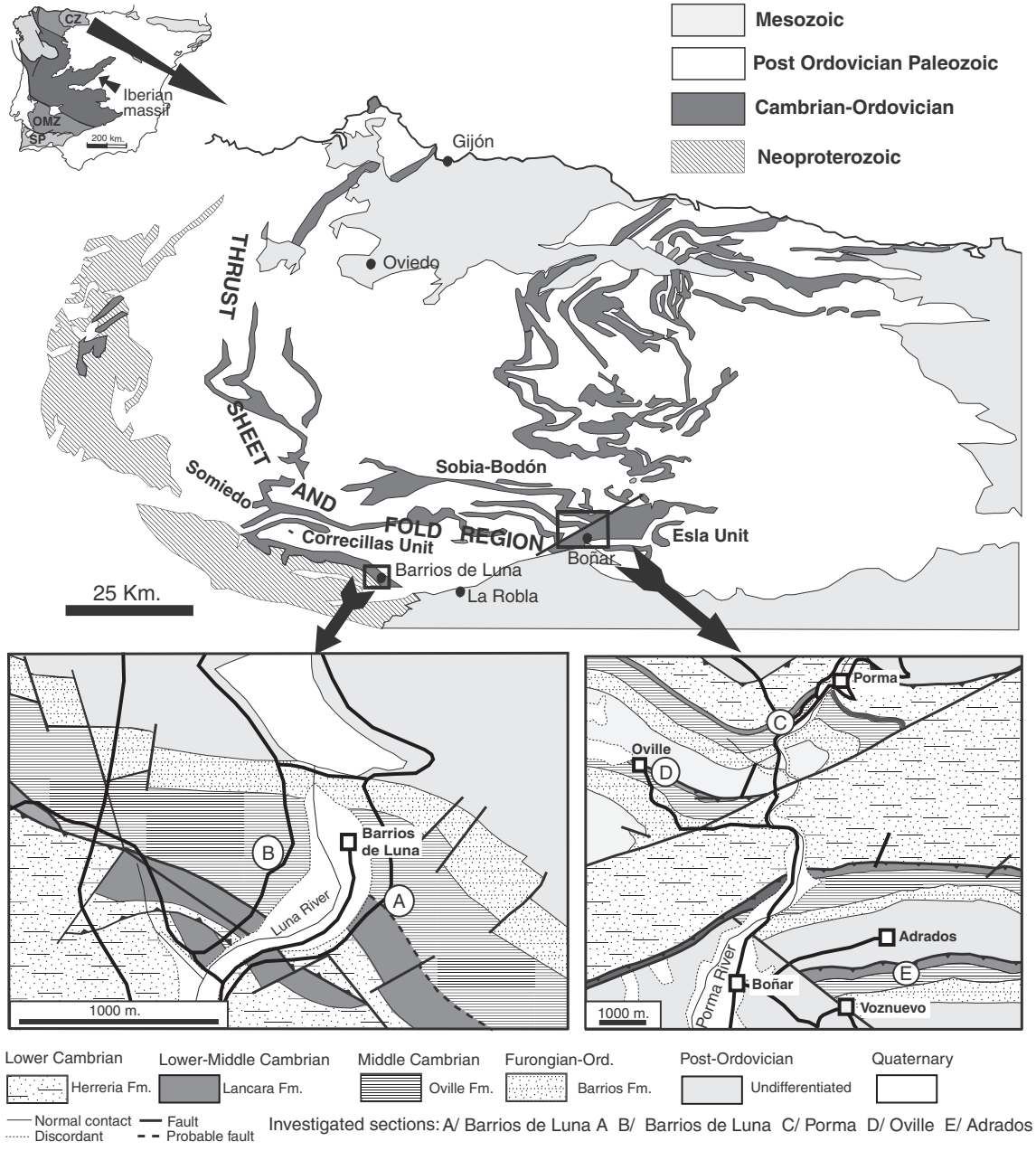


Fig. 1. Geological sketch map of the Cantabrian Zone, showing the main geological units and the location of the Porma and Barrios de Luna areas. In the detailed geological maps of the Porma and Barrios de Luna areas are shown the locations of the sections studied. Based on Aramburu et al. (2006) and other publications.

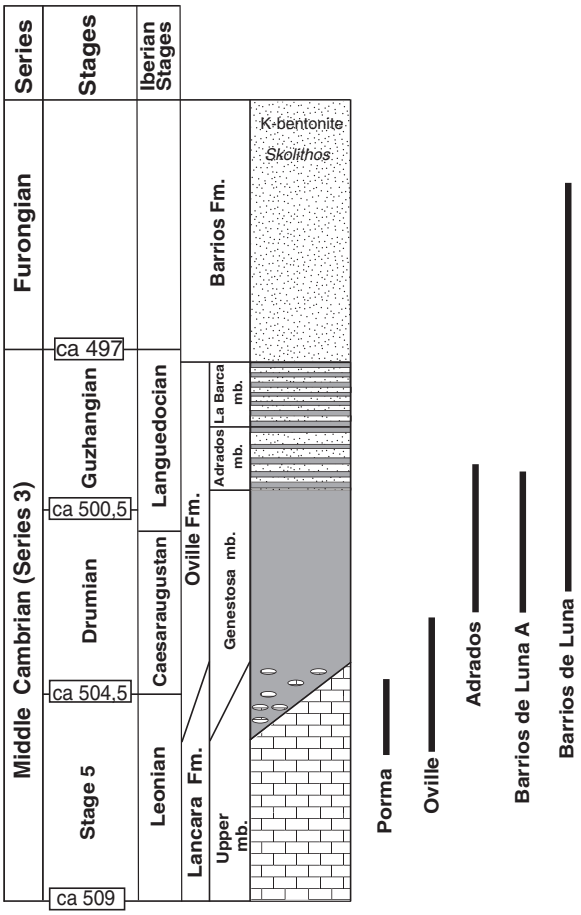


Fig. 2. Cambrian lithostratigraphic units in the study area, and relative location of the columns of sections analysed in this study.

regional Ovetian stage (Sdzuy, 1971). The Herrería Formation is conformably overlain by carbonate rocks attributed to the Láncara Formation. These were extensively studied by Zamarreño (1972). The Láncara Formation has two members: the lower includes early Bilbilian or Toyonian age archaeocyathids (Debrenne and Zamarreño, 1970; Perejón and Moreno-Eiris, 2003), while the upper, in contact by an erosive unconformity, includes Leonian trilobites (Sdzuy, 1968; Gozalo et al., 2003b). The overlying Oville Formation (Compte, 1937) comprises the Genestosa, Adrados, and La Barca members (Aramburu and García-Ramos, 1993). Of these, only the Genestosa Member contains abundant and diagnostic trilobites (Sdzuy, 1961, 1968, 1995). Sdzuy (1968) and Zamarreño (1972), based on the occurrence of trilobites, consider that the base of the Oville Formation is diachronous. The Barrios Formation, overlying the Oville Formation, was recently considered Furongian–lower Ordovician (Arenigian). Acritarchs from a sample of the lower Member (Matosa Member) include an assemblage that correlates with the *Leptoplastus* and the *Peltura* trilobite zones of the Furongian (Albani et al., 2006, 2007). New data presented in the present work from the Barrios de Luna section indicates a middle Cambrian–Furongian age for the levels preceding the occurrence of sandstones with *Skolithos* and the first level of K-bentonite (Aramburu et al., 2006).

3. Material and methods

Samples from the Oville Formation were collected in three sections in the Boñar area (the Porma and Oville sections (Figs. 1–4) in the Sobia-Bodon Unit, and the Adrados section (Figs. 1, 2, 5) in the Esla Unit), and in two sections in the Barrios de Luna area (Barrios de Luna A and Barrios de Luna: Figs. 1, 2, 6, 7) in the Correcillas Unit. The stratigraphic distribution of the samples, and the occurrence and abundance of acritarch species are illustrated graphically in Figs. 3–7.

In general, the samples from the Boñar area contain abundant and diverse well preserved acritarchs, without evidence of breakage or degradation. The colour of the acritarchs is dark yellow to orange (TAI 2, sensu Hayes et al., 1983). Samples of the Barrios de Luna area have a similar preservation but with greater thermal alteration. The colour of the acritarchs is orange to light brown (TAI 2–3).

The oldest acritarch assemblages are included in the levels of glauconitic mudstones with calcareous nodules at the base of the Genestosa Member in the Porma and Oville sections. The upper part of this Genestosa Member includes dark gray to olive green shale and mudstones with abundant organic matter providing abundant acritarchs. Exposures of these levels are poor, and sediments are often weathered. For example, the slightly weathered shale of the Genestosa Member in the Barrios de Luna section (Fig. 7) gave negative results, whereas unweathered exposures of the same levels in the Barrios de Luna A section provide abundant acritarchs (Fig. 6).

Samples from the Adrados Member consist of dark gray to olive green shale and mudstones, and those from the La Barca Member and La Matosa Member of the Barrios Formation include dark gray to green shale and mudstones. Filamentous sheaths, presumably deriving from oscillatoriacean cyanobacteria, and *Tasmanites* are abundant in some samples.

The samples were processed using standard palynological acid digestion techniques (see Vidal, 1988). Samples of ca. 50 g were macerated in 40% hydrofluoric acid, and the resulting residue was boiled in concentrated hydrochloric acid and then filtered through 15 and 20 μm mesh membranes. Permanent mounts were prepared by mixing precipitate with epoxy resin (Petroepoxy 154) on glass slides. Slides

were examined and photographed under transmitted light with a Zeiss Axio Imager M1 microscope equipped with a computerized Axiocam HRc microcamera.

4. Acritarch biostratigraphy

The biostratigraphic study of the Oville Formation presented here is based on detailed sampling for acritarchs in five sections, providing information on the first appearance and last presence of diagnostic taxa.

The lower part of the Genestosa Member is well exposed in the Porma and Oville sections (Figs. 3 and 4), where contact with the underlying Láncara Formation is gradual, with a decreased in levels with carbonate nodules and an increase in shales and mudstones. In the Adrados section (Fig. 5), the upper part of the Genestosa Member is well exposed, characterized by massive shale and mudstones with sandstone levels at the top (*Simula* Sandstone) marking a gradual transition to the Adrados Member. Observations made in a section in Vozmediano, indicate a possible faulted contact between the Láncara and Oville Formations, with the presence of diabase dikes. The first records of acritarchs in the Adrados section are located below the *Simula* Sandstone (Fig. 5). Similar levels from the Barrios de Luna A section (Fig. 6) are included in the *Solenopleuropsis marginata* Zone (lower Languedocian sensu Álvaro and Vizcaïno, 1998).

The Barrios de Luna sections (Figs. 6, 7) is the closest to completeness. It includes the Genestosa, Adrados, and La Barca Members of the Oville Formation and the overlying Barrios Formation (the La Matosa Member). In this section, a generally faulted contact between the Oville Formation and the underlying Lancara Formation has cut out lower beds of the former to a greater or lesser extent. (Fig. 1, and Aramburu et al., 2006).

Palacios (2008), in a preliminary study, recognized five middle Cambrian acritarch interval zones (IMC1–IMC5). Here, a new zone (IMC6) is recognized in the middle Cambrian (Cambrian Series 3), and one lower Furongian acritarch assemblage is identified in the middle part of the Matosa Member of the Barrios Formation in the Barrios de Luna section. This zonation is described in greater detail in the present paper, and the upper limit of each zone is marked by the FAD of the species that define the following Zone.

4.1. The IMC1 Zone

This zone was defined in the Vallehondo Formation, Cambrian of southern Spain (Palacios et al., 2006; Palacios, 2008), by the first appearance of *Comasphaeridium silesiense*, a species with a broad stratigraphic range and with the first appearance in the *Paradoxides oelandicus* Zone in Poland (Moczydłowska, 1998, 1999). Other species with a first appearance close to that of *C. silesiense* in the lower part of the Vallehondo Formation in southern Spain are *Tubulosphaera perfecta* and *Eliasum llaniscum*, and at higher levels within the same zone there appear *Retisphaeridium dichamerum*, *Comasphaeridium longispilosum*, and *Comasphaeridium francinae*.

In the study area, the oldest acritarch assemblages included in this zone are in the Porma section (Fig. 3) in levels that include Upper Leonian trilobites (*Paradoxides asturianus* and *Tonkinella* aff. *breviceps*, among others, Gozalo et al., 2003b). The acritarch assemblages include *Comasphaeridium francinae* Jachowicz-Zdanowska, 2013 (Plate VI, 1–7), *Comasphaeridium silesiense* Moczydłowska, 1998 (Plate I, 6), *Comasphaeridium longispilosum* Hagenfeldt, 1989 (Plate I, 4), *Eliasum llaniscum* Fombella, 1977 (Plate VIII, 1), *Liepaina plana* Jankauskas &

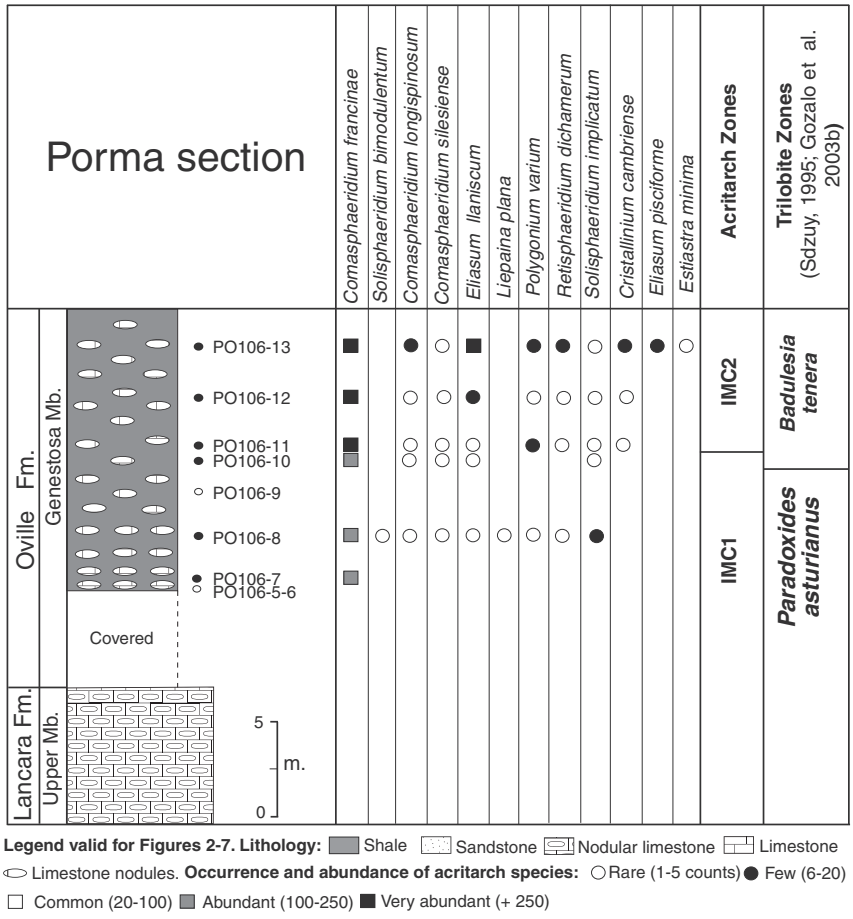


Fig. 3. Lithostratigraphic column of the Porma section showing location of the acritarch samples. UTM data zone ED50 30T 312081, 4754754; 311946, 4754634. Black discs indicate positive samples, and white, barren. Figure legend applicable to Figs. 2–7.

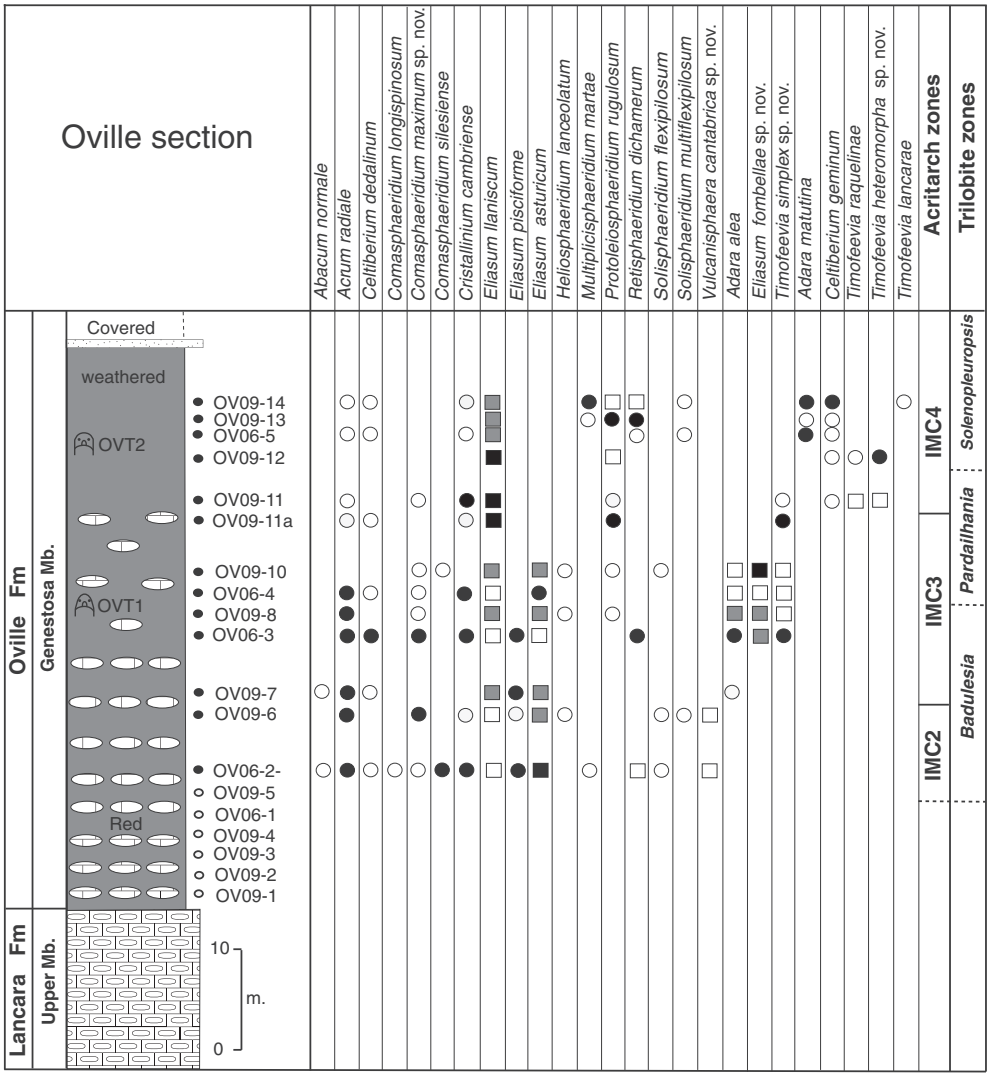


Fig. 4. Lithostratigraphic column of the Oville section. UTM data zone ED50 30T 308757, 4753322; 308861, 4753157.

Volkova, 1979 (Plate I, 1), *Polygonium varium* (Volkova, 1969) Sarjeant & Stancliffe 1994 (Plate I, 2), *Retisphaeridium dichamerum* Staplin, Jansonius & Pocock 1965 (Plate II, 1), *Solisphaeridium implicatum* (Fridrichsone, 1971) Moczydłowska, 1998 (Plate I, 3), and *Solisphaeridium bimodulentum* Moczydłowska, 1998 (Plate I, 7).

C. francinae was described in open nomenclature by Martin in Martin and Dean (1984) with a first appearance recorded near the top of the Chamberlain Brook Formation below a level that contains *Badulesia* aff. *B. tenera*, *Paradoxides eteminicus* and *Hartella terranovica* (Martin and Dean, 1988, Fig. 3), included in the AO-1 acritarch zone (equivalent to the *Hartella* Zone). This zone also includes scarce *E. llaniscum* and *R. dichamerum*, without *Cristallinium cambriense*. A similar assemblage with *C. francinae*, *E. llaniscum*, and *R. dichamerum* is recorded in New Brunswick in the Forest Hills Formation in levels that contain *Paradoxides* cf. *eteminicus* (Palacios et al., 2012a). Other occurrences of *C. francinae* are in north-west Wales in the Nant-y-big Formation in levels of the *Tomagnostus fissus* Zone (Young et al., 1994), in levels that contain *R. dichamerum*, *C. cambriense*, and *Heliosphaeridium? llynensis*. Similar assemblages without *C. cambriense* occur in the Dugald Formation in Nova Scotia (Palacios et al., 2012b).

C. longispilosum is recorded in Baltica in the *A. oelandicus* Super Zone (Hagenfeldt, 1989), in Wales in the Nant-y-big Formation, *P. paradoxissimus* Zone (Young et al., 1994), and southeastern Turkey in the top of the Koruk Formation and bottom of the Sosink Formation in levels above the *Pardailhania* Zone and levels with *Solenopleuropsis* (Dean et al., 1997). In southern Spain, this species is restricted to the *C. silesiense* Zone (Palacios et al., 2006), equivalent to the IMC1 Zone (Palacios, 2008).

E. llaniscum (Plate VIII, 1) is a problematic species (see systematic description) with a broad stratigraphic range (Fig. 7). The lower stratigraphic range is mostly given as the uppermost lower Cambrian–middle Cambrian (e.g., Molyneux et al., 1996) or middle Cambrian (e.g., Moczydłowska, 1999). *S. bimodulentum* appears in the *Paradoxides oelandicus* Zone in Poland (Moczydłowska, 1998). *S. implicatum* appears in Baltica in the Vergale horizon, and is very abundant in the Vallehondo Formation in southern Spain in the lower Cambrian *Heliosphaeridium notatum* Zone, equivalent to the Vergale Horizon (Palacios et al., 2006), and in the IMC1 Zone (Palacios, 2008).

L. plana and *P. varium* are restricted in Baltica to Vergale and Kibartai (see Moczydłowska, 1998). Recently, both have been recorded in the *Protolenus* Zone in Avalonia (Hanford Formation, Palacios et al., 2012a).

All the above species, except *S. bimodulentum* and *L. plana*, continue into the next zone, and *E. llaniscum* and *R. dichamerum* have a broad stratigraphic range (Fig. 8). Fig. 9 shows the correlation of this zone with Baltica and Avalonia.

The IMC1 Zone is equivalent in part to the Leonian regional stage, roughly equivalent to Stage 5 (Gozalo et al., 2013). In the Vallehondo Formation, where the zone is defined, trilobites are rare,

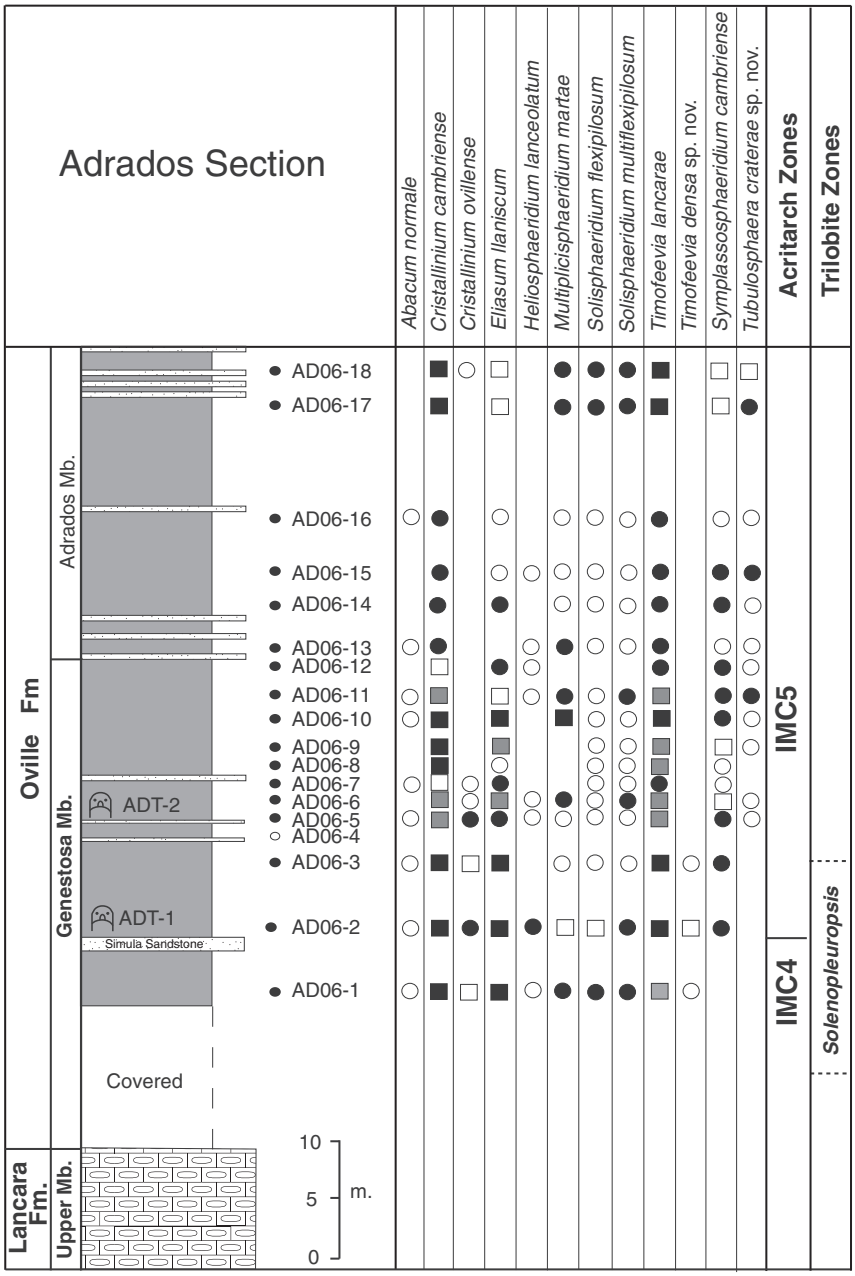


Fig. 5. Lithostratigraphic column of the Adrados section. UTM data zone ED50 30T 314802, 4749342; 314335, 4749159.

but included in the middle part are *Paradoxides* sp. (Bard, 1964) and *Parasolenopleura* sp. (Liñán et al., 1996). Levels recording the start of the zone include idiomorphic zircons. Moczydłowska, 1999 suggests the FAD of *E. llaniscum* and *C. silesiense* for the beginning of the middle Cambrian. I therefore consider that the IMC1 Zone has great potential to establish the globally lower boundary of Stage 5 (Cambrian Series 3).

4.2. The IMC2 Zone

This zone, characterized by a significant increase in the diversity of acritarchs, was originally defined (Palacios et al., 2006; Palacios, 2008) as a zone characterized by the first occurrence of *Cristallinium cambriense*. The base of this zone is identified in the Porma section (Fig. 3), and is well represented, including its upper limit, defined on the Oville section (Fig. 4). In this paper, the IMC2 Zone is redefined as an assemblage zone, characterized by the first appearance of the cosmopolitan acritarchs *C. cambriense* Vanguestaine, 1978 (Plate II, 2, 3), *Eliasum asturicum* Fombella, 1977 (Plate VIII, 3–7), and species of the genus *Vulcanisphaera* (*Vulcanisphaera cantabrica* sp. nov.) (Plate XV, 1–6). Other species that first appear in this zone are: *Abacum normale* Fombella, 1978 (Plate II, 7), *Celtiberium dedalinum* Fombella, 1978 (Plate II, 6), *Heliosphaeridium lanceolatum* (Vanguestaine 1974) Moczydłowska, 1998 (Plate III, 6), *Multiplicisphaeridium martae* Cramer and Díez, 1972(Plate III, 7), *Solisphaeridium flexipilosum* (Slavíková, 1968) Moczydłowska, 1998 (Plate I, 8), *Solisphaeridium multiflexipilosum* (Slavíková, 1968) Moczydłowska, 1998 (Plate I, 9). Other species that appear, and that have only been found to be present in the Oville Formation, are *Acrum radiale* Fombella, 1977 (Plate II, 5), *Comasphaeridium maximum* sp. nov. (Plate VII, 1–4), *Eliasum pisiformis* Fombella, 1977 (Plate VIII, 2), and *Protoleiosphaeridium rugulosum* (Fombella, 1978) Fensome et al., 1990 (Plate II, 4). This assemblage zone is equivalent in part to the *Badulesia* Zone, and the FAD of *C. cambriense* in the Porma section is proximally coincident with the

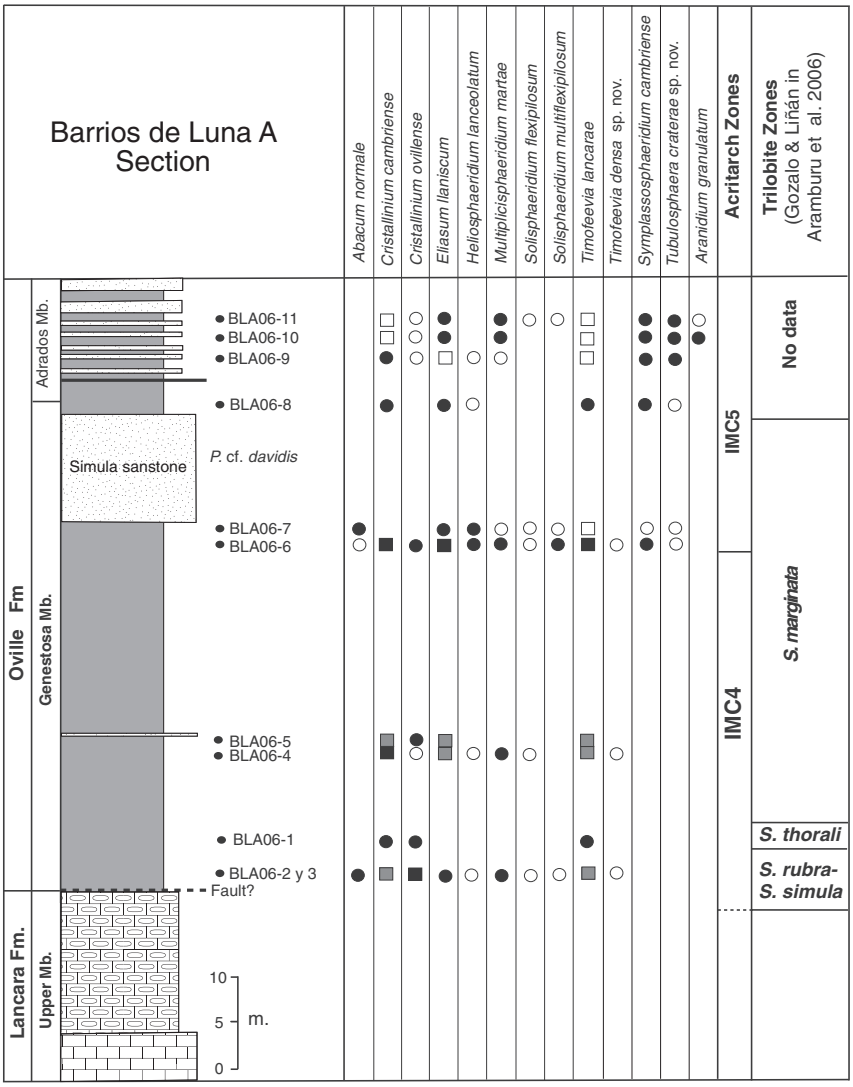


Fig. 6. Lithostratigraphic column of the Barrios de Luna A section. UTM data zone ED50 30T 265852, 4747676; 265938, 4748330.

FAD of *Badulesia tenera* (Fig. 3). The top of the zone is below a level included in the IMC3 Zone that contains *B. granieri*, *Agraulos* sp., and *Parabailiella?* sp. in the Oville Section (Plate XVI, 1, 2, 4 and Fig. 4). In Avalonia, the first appearances of the *Vulcanisphaera* species (*Vulcanisphaera lanugo*) and *C. cambriense* indicate the A0 acritarch Zone (Martin and Dean, 1988, Fig. 3) and occur near the base of the Manuels River Formation in levels that contain *Paradoxides hicksii*, the *P. hicksii* Zone. In the Bourinot belt (Cape Breton Island), *V. cantabrica* sp. nov. (see the synonymies), *C. cambriense*, and *E. asturicum* appear near the top of the Dugald Formation (Palacios et al., 2012b). In southern Spain, these species appear in the lower part of the Playón Formation (Palacios et al., 2006). In Ireland in the Booley Bay Formation, Vanguestaine and Brück (2008) referred to the occurrence of *C. cambriense* and *V. lanugo* in the BB1 assemblaged that they correlated with the lower A2 zone of E. Newfoundland (= top Drumian, *P. punctuosus* Zone — mid Guzhangian, *L. laevigata* Zone), but they noted that some species occurred at lower levels in Newfoundland. Brück and Molyneux (2011), took account of these lower occurrences and ranges in Newfoundland to depict the BB1-bearing rocks extending from about the base of the *T. fissus* Biozone into the lower part of the *P. forchhammeri* Superzone (Drumian to lower Guzhangian). In Baltica, *C. cambriense* and *H. lanceolatum* appear in the SK1 assemblage, correlated with the lower *P. paradoxissimus* Zone (Volkova and Kiryanov, 1995). The oldest occurrences of *C. cambriense* in Baltica are either not contrasted or their assignation is problematic. Recent research in northern Norway, the Digermul Peninsula, has revealed the presence of *C. cambriense* and *Vulcanisphaera* species from basal levels of the Kistedal Formation (K1), which includes trilobites indicative of the upper *P. oelandicus* to the lower *P. paradoxissimus* zones (Palacios unpublished data). *C. dedalinum* is scarce and has a broad stratigraphic range. The lowest occurrence has been recorded from the Celtiberian Chains at levels below the Leonian (Palacios and Moczydłowska, 1998), and the highest at levels no higher than the *P. paradoxissimus* Superzone (Brück and Vanguestaine, 2004; Brück and Molyneux, 2011). *H. lanceolatum*, *S. flexipilosum*, and *S. multiflexipilosum* are known from levels bracketed between the *P. paradoxissimus* and *P. forchhammeri* zones (Moczydłowska, 1998). *M. martae* is a problematic species with lowest occurrences in the *E. oelandicus* Zone in Silesia (Moczydłowska, 1998, 1999) and the *C. silesiense* Zone (IMC1) in southern Spain (Palacios et al., 2006). However, the specimens illustrated by Moczydłowska (1998, 1999) and those included in the *C. silesiense* Zone (Palacios et al., 2006 and personal observations) could constitute a new species with diagnostic characters very similar to *H. notatum*, with heteromorphic simple and bifurcate processes different from those of *M. martae* (Plate III, 7), with columnar heteromorphic processes and rounded distal terminations as described in the type material from the Oville Formation (Cramer and Díez, 1972).

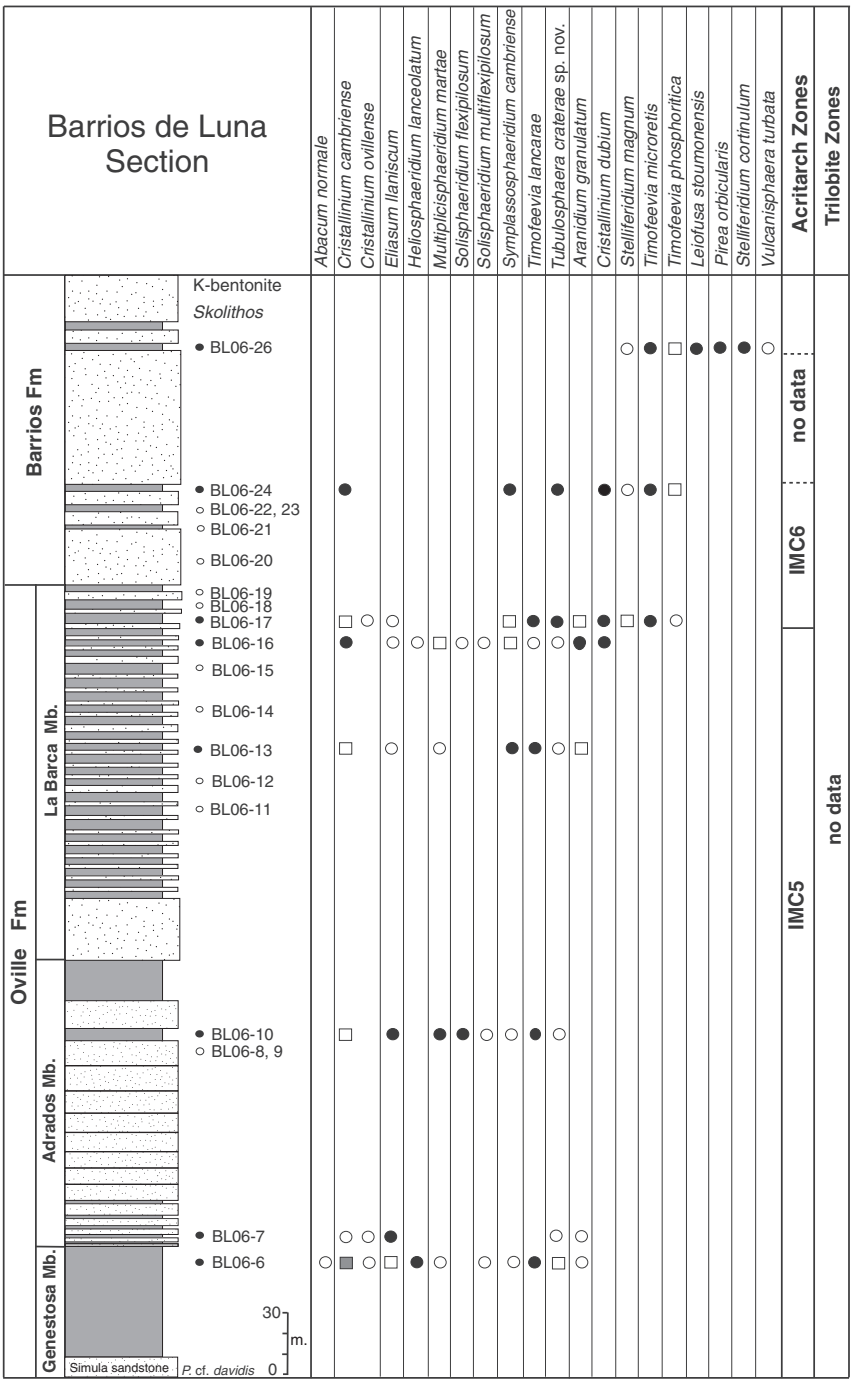


Fig. 7. Lithostratigraphic column of the Barrios de Luna section. UTM data zone ED50 30T 266323, 4747494; 266498, 4747685.

The IMC2 Zone is equivalent to the lower Caesaraugustian regional stage (*Badulesia* Zone) (Figs. 8, 9) and is correlated with the A0 Zone in Newfoundland equivalent to the *H. hicksii* Zone (Martin and Dean, 1988, Fig. 9). Fletcher (2006) referred to *Acidisus atavus* (*Ptychagnostus atavus* in the middle part of the *H. hicksii* Zone, that correlated with an interval bracketed between the top of the *Badulesia tenera* Zone and the lower part of the *Pardailhania* Zone (Fletcher, 2006, Fig. 18). The base of the Drumian is defined by a GSSP coinciding with the FAD of *Ptychagnostus atavus* (Babcock et al., 2007). Acritarch data are in agreement with Fletcher's correlations, so that the base of the Drumian in Oville would be in the *Badulesia* Zone equivalent to the IMC2 Zone. This position is slightly lower than that proposed by Gozalo et al. (2011) at the base of the *Pardailhania* Zone.

4.3. The IMC3 Zone

In Spain, this association was recognized as the *Adara* Zone in the Playón Formation (Palacios et al., 2006), and later renamed as the IMC3 Zone (Palacios, 2008). The presence of new diagnostic species allows a better characterization of this zone.

The first appearance of *Adara alea* Martin in Martin and Dean, 1981(Plate III, 1, 2), *Eliasum fombellae* sp. nov. (Plate VIII, 8–16), and *Timofeevia simplex* sp. nov. (Plate XIII, 1–4) defines the base of the zone. The upper part of the zone also includes the last appearance of *E. asturicum*, *E. fombellae* sp. nov., and *A. alea*. Consequently, IMC3 can also be considered to be a range zone (*Adara alea* Zone). All the species that appear in the IMC2 Zone except *V. cantabrica* sp. nov. are present

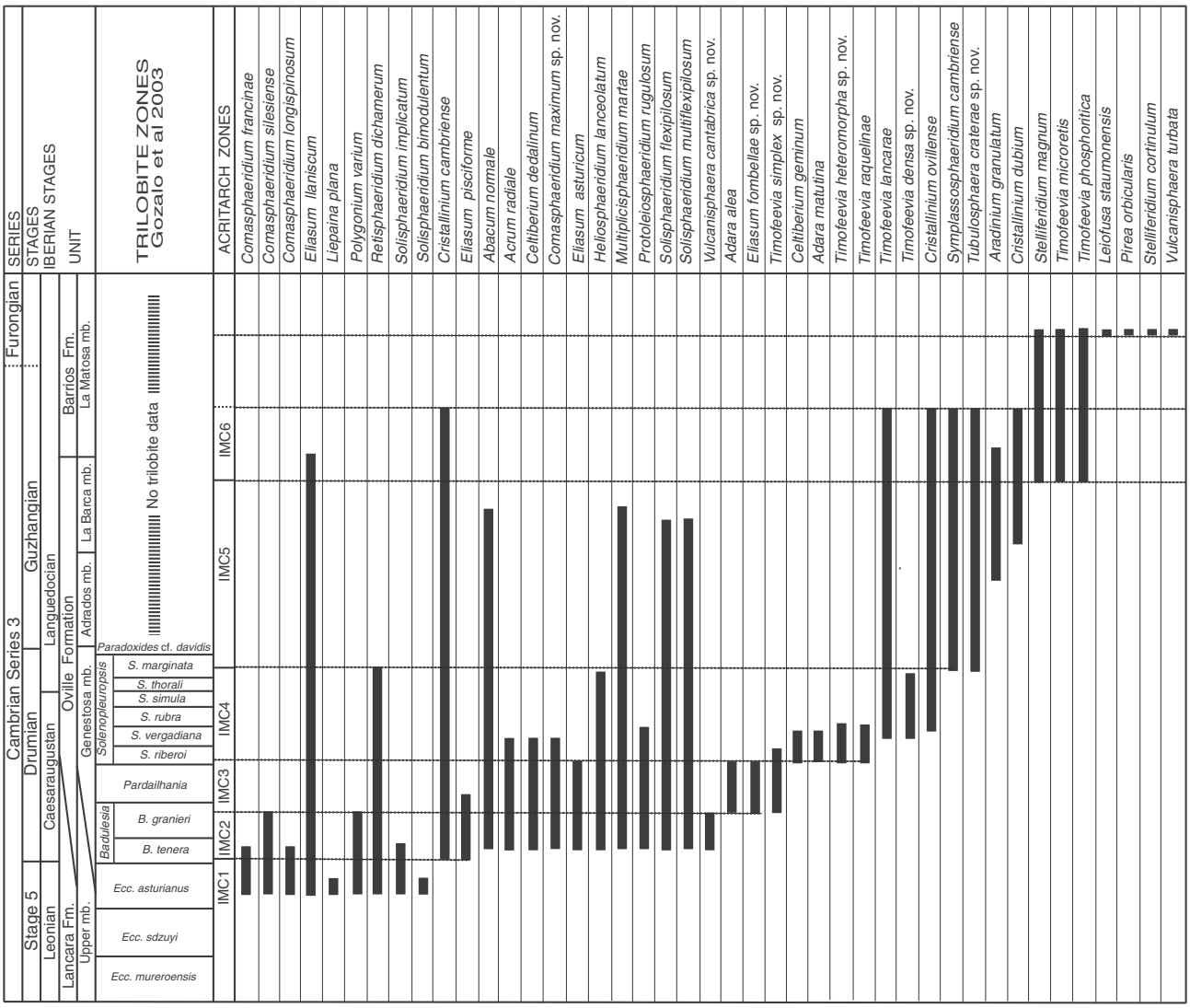


Fig. 8. Stratigraphic ranges of acritarchs in the Oville and Barrios formations. Acritarch biozones and their relationships with trilobite zones.

(Fig. 8). In the Oville section (Fig. 4) the first record of *A. alea* occurs close to levels that contain *Badulesia granieri, Agraulos* sp., and *Parabailiella*?sp. (Plate XVI, 1, 2, 4), and the last appearance is close to a level that contains *Solenopleuropsis* sp. (Plate XVI, 3). The IMC3 Zone thus corresponds to an interval within the uppermost lower Caesaraugustian, top of the *Badulesia* Zone, and the *Pardailhania* Zone (Gozalo et al., 2003b, 2011).

In Avalonia, the first appearance of *A. alea* and *E.* cf. *asturicum*, included in the synonymy of *E. fombellae* sp. nov. (see Section 5 Systematics), occurs in the Manuels River Formation close to the highest occurrence of *Paradoxides hicksii*, and the last occurrence of *A. alea* at Manuels River is 6 m below the occurrence of *Paradoxides davidis* (Martin and Dean, 1988, Figs. 3 and 7). In Random Island, the last occurrence of *A. alea* coincides with the highest occurrence of *Paradoxides hicksii* (Martin and Dean, 1981, Fig. 3). In Wales, *A. alea* is referred to in the middle part of the Nant-y-big Formation, the *Tomagnostus fissus* Zone (Young et al.1994). In Morocco, Vanguestaine and Van Looy (1983) referred to *Celtiberium* cf. *geminum* (in my opinion, synonymous with *A. alea*) in a calcareous sandstone unit and in the lower part of the overlying unit of green siltstone with *Parasolenopleura* cf. *cristata*.

Other records of *A. alea* not contrasted with trilobites are in the Upper Cambrian in Silesia, the Sosnowiec Formation (Moczydłowska, 1998), and appear with *C. randomense*, a diagnostic species of the upper Cambrian. However *C. randomense* is a problematic species that can be confused with flattened specimens of *E. fombellae* (Plate VIII, 14, 15), as will be discussed below in Section 5 on Systematics. Jachowicz-Zdanowska (2010) considers the associations with *Adara* in the Sosnowiec Formation to be typical for the middle Cambrian *Paradoxides oelandicus* and *Paradoxides paradoxissimus* Zones. Recently Jachowicz-Zdanowska (2011) cited *A. alea* in Assemblage III of the middle Cambrian from the Stalowa Wola–Lubaczów area in Poland. In the Ardennes, France, Vanguestaine and Leonard (2005) referred to *A. alea* in the Sautou Formation.

Gozalo et al. (2011) propose placing the base of the Drumian in Spain at the base of the *Pardailhania* Zone. However, the correlations with acritarchs (see above) are more consistent with a location at the lower Caesaraugustian (the *Badulesia* Zone, Fig. 9).

4.4. The IMC4 Zone

In Spain, this association was recognized as *Timofeevia lancarae* Zone in the Playón Formation (Palacios et al., 2006), and later renamed as the IMC4 Zone (Palacios, 2008) and erroneously correlated with the lower A2 Zone (Martin and Dean, 1988), both characterized by the first appearance of *T. lancarae*. An important problem in middle Cambrian acritarch biostratigraphy is the incorrect identification of *T. lancarae*

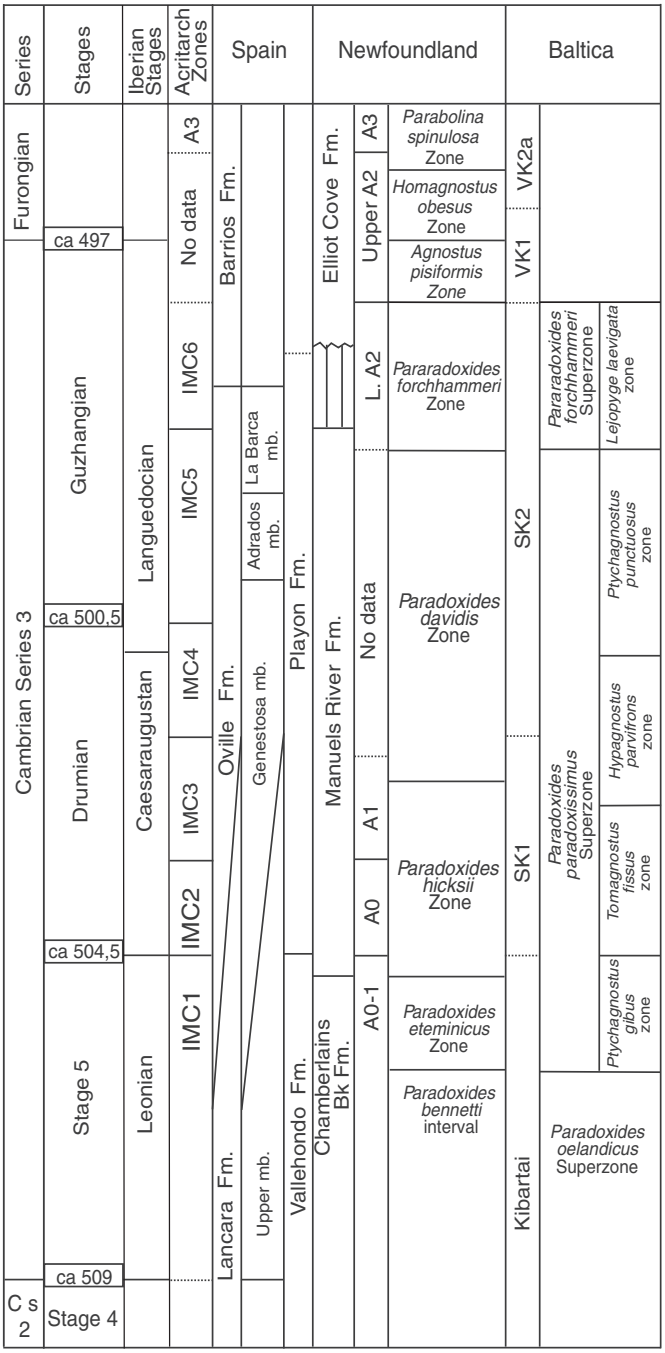


Fig. 9. Correlation between acritarch zones in Spain (Cantabrian Mountains – this paper – and Zafra area sensu Palacios et al., 2006), Newfoundland, and Baltica. Newfoundland data from Martin and Dean (1988), and Baltica from Volkova and Kiryanov (1995).

(see Section 5 Systematics). For example, the diagnostic characters of the specimens assigned to *T. lancarae* in the lower A2 Zone in Martin and Dean (1988) do not correspond to *T. lancarae* sensu Cramer and Díez (1972). Palacios et al. (2009) include most of the specimens of *T. lancarae* illustrated in Martin and Dean (1988) and Welsch (1986) in the synonymy of *Stelliferidium magnum*, a form that appears in the younger IMC6 Zone described below in this paper.

In this context, the IMC4 Zone has no comparisons with the zonation erected in Newfoundland, likely as a result of an important hiatus in that area. This would explain the rare presence of *Eliasum llaniscum* in the lower A2 Zone in Newfoundland, while this species is very abundant in the IMC4 Zone, decreasing sharply in abundance in the upper part of IMC5, to disappear close to the base of IMC6 (Figs. 5–7). A detailed sampling of the Oville, Adrados, and Barrios de Luna sections allows for a better characterization of the ICM4 Zone, as will be described below.

The lower part of this zone in the Oville section (Fig. 4), includes the first appearance of species with very short ranges, such as *Adara matutina* Fombella, 1977 (Plate III, 3, 5), *Celtiberium geminum* Fombella, 1977 (Plate III, 4), *Timofeevia heteromorpha* sp. nov. (Plate XI, 1–6), and *Timofeevia raquelinae* (Cramer and Díez, 1972) Cramer and Díez, 1979 (Plate XIII, 5, 6), and others with a broad stratigraphic range, such as *Timofeevia lancarae* (Cramer and Díez, 1972) Vanguestaine, 1978 (Plate XII, 1–6), *Timofeevia densa* sp. nov. (Plate X, 1–6), and *Cristallinium ovillense* (Cramer and Díez, 1972) Martin 1981 (Plate IV, 3). Another important aspect of this zone is the great abundance (acme zone) of *E. llaniscum* and *C. cambriense*. The zone is equivalent to the Upper Caesaraugustian (the *Solenopleuropsis riberoi* to *S. simula* Zones).

The earliest records of specimens clearly assignable to *T. lancarae* (see Section 5 Systematics) are in the SK2 Zone in Baltica, equivalent to the *Paradoxides paradoxissimus* Zone (Volkova, 1990; Volkova and Kiryanov, 1995; Jankauskas, 2002). A similar assemblage to IMC4 with *C. geminum*, *T. lancarae*, and *C. ovillense* are recorded in the Sosink Formation southeastern Turkey (Erkmen and Bozdogan, 1981), and the earliest record of *T. lancarae* is recorded at levels between *Pardailhania* and *Solenopleuropsis* (transition between the Koruk and Sosink Formations, Dean et al., 1997), similar to the Oville section (Fig. 4). In the middle Cambrian Jince Formation of the Czech Republic, *T. lancarae* appears in levels assigned to the *Onymagnostus hybridus* Zone (Fatka et al., 2004). Some probably earliest records of *T. lancarae* with *Celtiberium* cf. *geminum* (*A. alea*, see above) occur in Morocco in levels that contain *Parasolenopleura* cf. *cristata* (Vanguestaine and Van Looy, 1983).

4.5. The IMC5 Zone

The lower part of this zone is defined here by the first appearance of *Symplassosphaeridium cambriense* Slavíková, 1968 (Plate IX, 1–4) and *Tubulosphaera craterae* sp. nov. (Plate XIV, 1–4). In the Barrios de Luna A section (Fig. 6), *S. cambriense* and *T. craterae* sp. nov. occur three metres below the *Simula* Sandstone at levels bracketed between the *Solenopleuropsis marginata* Zone and levels with *Paradoxides* cf *davidis* (lower Languedocian, Gozalo & Liñán in Aramburu et al., 2006). In the upper middle part of this zone, there appear *Aradinium granulatum* Welsch, 1986 (Plate IV, 1, 2) and *Cristallinium dubium* Volkova, 1990 (Plate V, 1). In the Adrados section (Fig. 5), the base of this zone is recognized in a similar position very close to the *Simula* Sandstone.

Slavíková (1968) described the species *Symplassosphaeridium cambriense* from the Jince Formation of the Czech Republic in levels assigned to the *Ellipsocephalus hoffi* sub-Zone or *Ellipsocephalus hoffi–Rejkocephalus* Abundance Zone sensu Fatka (2006), correlated with the upper Languedocian (Álvaro et al., 2004). Palacios (1997) reported this species (as coenobial acritarchs) from the Acón Formation, assigned to the Languedocian with abundant *A. granulatum* and *C. dubium* (Palacios, 1997, Palacios unpublished data). Erkmen and Bozdogan (1981) reported *Symplassosphaeridium* cf. *cambriense* from the Sosink Formation, Turkey and from the same unit, Dean et al. (1997) reported it (as coenobial acritarchs) in levels with *Solenopleuropsis* sp. In Nova Scotia (Palacios et al., 2009), *S. cambriense* occurs with *C. dubium* near the base of the MacLean Brook Formation in a level bracketed between the occurrence of *P. davidis* and *P. forchhammeri*. An assemblage that includes *A. granulatum*, *C. dubium*, and *Tubulosphaera craterae* sp. nov. (see the synonymies) is recorded in the MacMullin Formation Bourinot Belt (Palacios et al., 2012b) and in New Brunswick a similar assemblage occurs in the King Square Formation (Palacios unpublished data).

In eastern Finnmark, an assemblage that includes *A. granulatum* appears in the upper part of the *P. paradoxissimus* Zone (Welsch, 1986).

The upper part of the IMC5 Zone, which records the first appearance of *C. dubium*, is equivalent to the VK2 Zone of Volkova and Kiryanov (1995), correlated with the *P. forchhammeri* Zone (Volkova and Kiryanov, 1995).

4.6. The IMC6 Zone

This zone is characterized by the first appearance of *Stelliferidium magnum* Palacios in Palacios et al., 2009 (Plate IV, 4), *Timofeevia microretis* Martin in Martin and Dean, 1981(Plate IV, 5), and *T. phosphoritica* Vanguestaine, 1978 (Plate IV, 6, 7). The base of the zone is located in the Barrios de Luna section at the top of the La Barca Member of the Oville Formation.

In Newfoundland, *T. microretis* appears near the base of the Elliot Cove Formation, in levels with *Agnostus pisiformis* (Martin and Dean, 1988) in an assemblage that includes *Vulcanisphaera turbata* (Upper A2 Zone of Martin and Dean, 1988). In the Mira area, Nova Scotia, the first appearance of *T. microretis* occurs in levels that contain *Paradoxides forchhammeri* in assemblages that include *S. magnum* and *T. phosphoritica* (Palacios, personal observations). As previously indicated in the discussion of the IMC4 Zone (see also the discussion in Section 5 Systematics), the specimens illustrated as *T. lancarae* by Martin and Dean (1981, 1988) do not correspond to this species, and have been include in the synonymies of *S. magnum* and *S. Albani* (Palacios et al., 2009), so that this association is equivalent to the Lower A2 of Martin and Dean, 1988 in Avalonia. In eastern Finnmark, a similar assemblage that includes *T. lancarae* (included in the synonymies of *S. magnum* and *S. albani*, Palacios et al., 2009), *T. phosphoritica*, and *T.* cf. *microretis* is recorded in the A2 trilobite Zone, equivalent to the *P. forchhammeri* Zone (Welsch, 1986).

The low number of positive samples at levels from the lower Barrios Formation that contain this association does not allow further definition. The upper limit of this association is well defined in Avalonia by the first appearance of *Vulcanisphaera turbata* and *T. pentagonalis*, which mark the Upper A2 Zone of Martin and Dean (1988) bracketed between the *Agnostus pisiformis* and *Olenus* zones (Guzhangian–Furongian transition).

4.7. Upper Cambrian (Furongian) assemblages

The uppermost positive sample of the La Matosa Member of the Barrios Formation contains a diverse assemblage that includes the diagnostic acritarchs *Pirea orbicularis* Volkova, 1990 (Plate V, 3), *Vulcanisphaera turbata* Martin in Martin and Dean, 1981 (Plate V, 4), *Stelliferidium cortinulum* (Deunff) Deunff, Gorka & Rauscher 1974 (Plate V, 6), and *Leiofusa stoumonensis* Vanguestaine, 1973 (Plate V, 2). *L. staumonensis* is recorded in the lower part of the Elliot Cove Formation in the Manuels River and Random Island sections in strata bracketed between the *Olenus* and *Parabolina spinulosa* Zones (uppermost part of the upper A2 and A3b Zones). *Pirea orbicularis* is recorded in levels bracketed between the *Agnostus pisiformis* and *Parabolina spinulosa* Zones (Palacios et al., 2009). The first appearance of *S. cortinulum* in Baltica is in the Vorchin Horizon, equivalent to the *Parabolina* Zone (Volkova and Kiryanov, 1995), and a similar first appearance is recorded in eastern Newfoundland (RA4 Zone, Parsons and Anderson, 2000). In the Mira area, abundant and well preserved specimens of *S. cortinulum* appear in levels that contain *Parabolina spinulosa* (T. Palacios, unpublished data). The presence of *P. orbicularis*, *S. cortinulum* and *L. staumonensis* allows this assemblage to be correlated with the A3 Zone of Martin and Dean (1988) and VK2a of Volkova and Kiryanov (1995). Acritarchs from a sample of the lower Member (Matosa Member) in "Túnel Ordovícico del Fabar" (Albani et al., 2006) include an assemblage that correlates with the *Leptoplastus* and the *Peltura* trilobite zones of the Furongian.

5. Systematics

Acritarch taxa are described here in alphabetical order under the informal incertae sedis group Acritarcha Evitt, 1963. A full list of selected taxa identified in this study is given in Figs. 3–8, together with their stratigraphic occurrences and relative abundances. The following taxa are illustrated but not described below as their identification in this material is considered unproblematic: *Adara alea* Martin in Martin and Dean, 1981 (Plate III, 1, 2), *Adara matutina* Fombella, 1977 (Plate III, 3, 5), *Acrum radiale* Fombella, 1977 (Plate II, 5), *Abacum normale* Fombella, 1977 (Plate II, 7), *Aranidium granulatum* Welsch, 1986 (Plate IV, 1, 2), *Celtiberium dedalinum* Fombella, 1977 (Plate II, 6), *Celtiberium geminum* Fombella, 1977 (Plate III, 4), *Cristallinium cambriense* (Slavíková, 1968) Vanguestaine, 1978 (Plate II, 2, 3), *Cristallinium dubium* Volkova, 1990 (Plate V, 1), *Cristallinium ovillense* (Cramer and Díez, 1972) Martin in Martin and Dean, 1981(Plate IV, 3), *Comasphaeridium silesiense* Moczydłowska, 1998 (Plate I, 6), *Comasphaeridium longispinosum* Hagenfeldt, 1989 (Plate I, 4), *Eliasum llaniscum* Fombella, 1977 (Plate VIII, 1), *Eliasum asturicum* Fombella, 1977 (Plate VIII, 3–7), *Eliasum pisciforme* Fombella, 1977 (Plate VIII, 2), *Estiastra minima* Volkova 1969 (Plate I, 5), *Heliosphaeridium lanceolatum* (Vanguestaine 1974) Moczydłowska, 1998 (Plate III, 6), *Leiofusa stoumonensis* Vanguestaine, 1973 (Plate V, 2), *Liepaina plana* Jankauskas & Volkova in Volkova et al., 1979 (Plate I, 1), *Multiplicisphaeridium martae* Fombella, 1977 (Plate III, 7), *Pirea orbicularis* Volkova, 1990 (Plate V, 3), *Polygonium varium* (Volkova 1969) Sarjeant & Stancliffe 1994 (Plate I, 2), *Protoleiosphaeridium rugulosum* Fombella, 1978 (Plate II, 4) *Retisphaeridium dichamerum* Staplin, Jansonius & Pocock 1965 (Plate II, 1), *Solisphaeridium bimodulentum* Moczydłowska, 1998 (Plate I, 7), *Solisphaeridium implicatum* (Fridrichsone 1971) Moczydłowska, 1998 (Plate I, 3), *Solisphaeridium flexipilosum* (Slaviková) Moczydłowska, 1998 (Plate I, 8), *Solisphaeridium multiflexipilosum* (Slaviková) Moczydłowska, 1998 (Plate I, 9), *Stelliferidium cortinulum* (Deunff 1961a) Deunff, Gorka & Rauscher 1974 (Plate V, 6), *Stelliferidium magnum* Palacios in Palacios et al., 2009 (Plate IV, 4), *Timofeevia phosphoritica* Vanguestaine, 1978 (Plate IV, 6, 7), *Timofeevia raquelinae* (Cramer & Díez) Cramer and Díez, 1979 (Plate XIII, 5, 6), *Timofeevia microretis* Martin in Martin and Dean, 1981 (Plate IV, 6), and *Vulcanisphaera turbata* Martin in Martin and Dean, 1981 (Plate V, 4, 5).

The new species *Comasphaeridium maximum* sp. nov., *Eliasum fombellae* sp. nov., *Timofeevia simplex* sp. nov., *Timofeevia heteromorpha* sp. nov., *Timofeevia densa* sp. nov., *Tubulosphaera craterae* sp. nov., and *Vulcanisphaera cantabrica* sp. nov. are recognized. The diagnoses of the genus *Eliasum* and the species *Symplassosphaeridium cambriense* are emended, and additional remarks have been introduced on *Timofeevia*, its type species *Timofeevia lancarae*, and *Comasphaeridium francinae*

Repository: Palynological slides containing figured and representative material are stored with the collections of the Area de Paleontología of the Universidad de Extremadura, Badajoz. The accession numbers are referred in the explanations of the plates.

* The term "plate" used in systematic descriptions is exclusively morphological, without taxonomic implications.

Group: ACRITARCHA Evitt, 1963 (*incertae sedis*)

Genus ***Comasphaeridium*** Staplin, Jansonius & Pocock 1965 emend. Sarjeant & Stancliffe, 1994

Type species: *Comasphaeridium cometes* (Valensi, 1949) Staplin et al., 1965.

Comasphaeridium francinae Jachowicz-Zdanowska, 2013 (Plate VI, 1–7)

1979 *Comasphaeridium filiforme* Fombella, Lamina III, 47 (nomen nudum)

1984 Acritarch gen. et sp. nov. Martin in Martin & Dean, Plate 57.1, 10, 17–19

1988 Acritarch gen. et sp. nov. Martin in Martin & Dean – Martin & Dean, Plate 2, 4

1994 Acritarch gen. et sp. nov. Martin in Martin & Dean – Young et al., Fig. 11, e

2008 Acritarch gen. et sp. nov. Martin in Martin & Dean – Palacios, Fig. 3, B

2012 Acritarch gen. et sp. nov. Martin in Martin & Dean – Palacios et al., 2012b Fig. 6, D, E

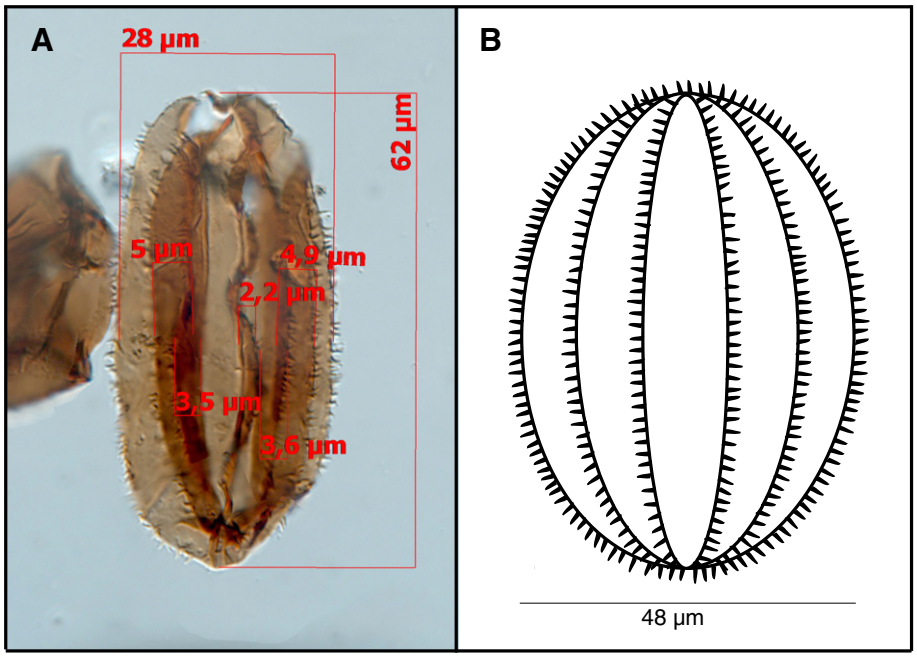


Fig. 10. Approximate reconstruction of the original shape form of *Eliasum fombellae* sp. nov. holotype. Flattening is limited to longitudinal folds that present their greatest width in the equatorial plane. **(A)** Holotype showing the measurements of the folds in Ecuador **(B)** Reconstruction by unfolding of the flattened areas at the equator.

2013 *Comasphaeridium francinae* n. sp. Jachowicz-Zdanowska, Pl. XXXI, 10,11,14

Dimensions: Vesicle width 3–9 µm (mean 5.18 µm). Process length 4–11 µm (mean 7.65 µm). (Based on 56 individual well preserved specimens.)

Description: Based on observations of more than one thousand well preserved specimens, both solitary and in clusters. The description of the colonial specimens (Pl. VI, 1–2) correspond to Acritarch gen. et sp. nov. (Martin in Martin and Dean, 1984), where it is stated, however, that "specimens are never found isolated". In the material analysed from the Oville Formation, colonial forms are observed, as described by Martin, but also individual specimens. In the material analysed, there is a process of individualization of the specimens in the mucilaginous colony, manifested by a progressive detachment and development of the processes (Plate VI, 1, 2). The result is their individualization, leading to morphology typical of *C. francinae* (Plate VI, 3–7). Individual specimens (Pl. VI, 6,7) correspond to *Comasphaeridium filiforme* sp. nov., which as illustrated by Fombella, 1979, but not formally described and considered a nomen nudum by Fensome et al. (1990). Frequently the vesicle of the specimens is distorted by pyrite growth (Plate VI, 3, 4).

Stratigraphic occurrence: Present record, IMCI, IMC2 zones. Southern Spain, top of the Vallehondo Formation IMC1 Zone (Palacios, 2008).

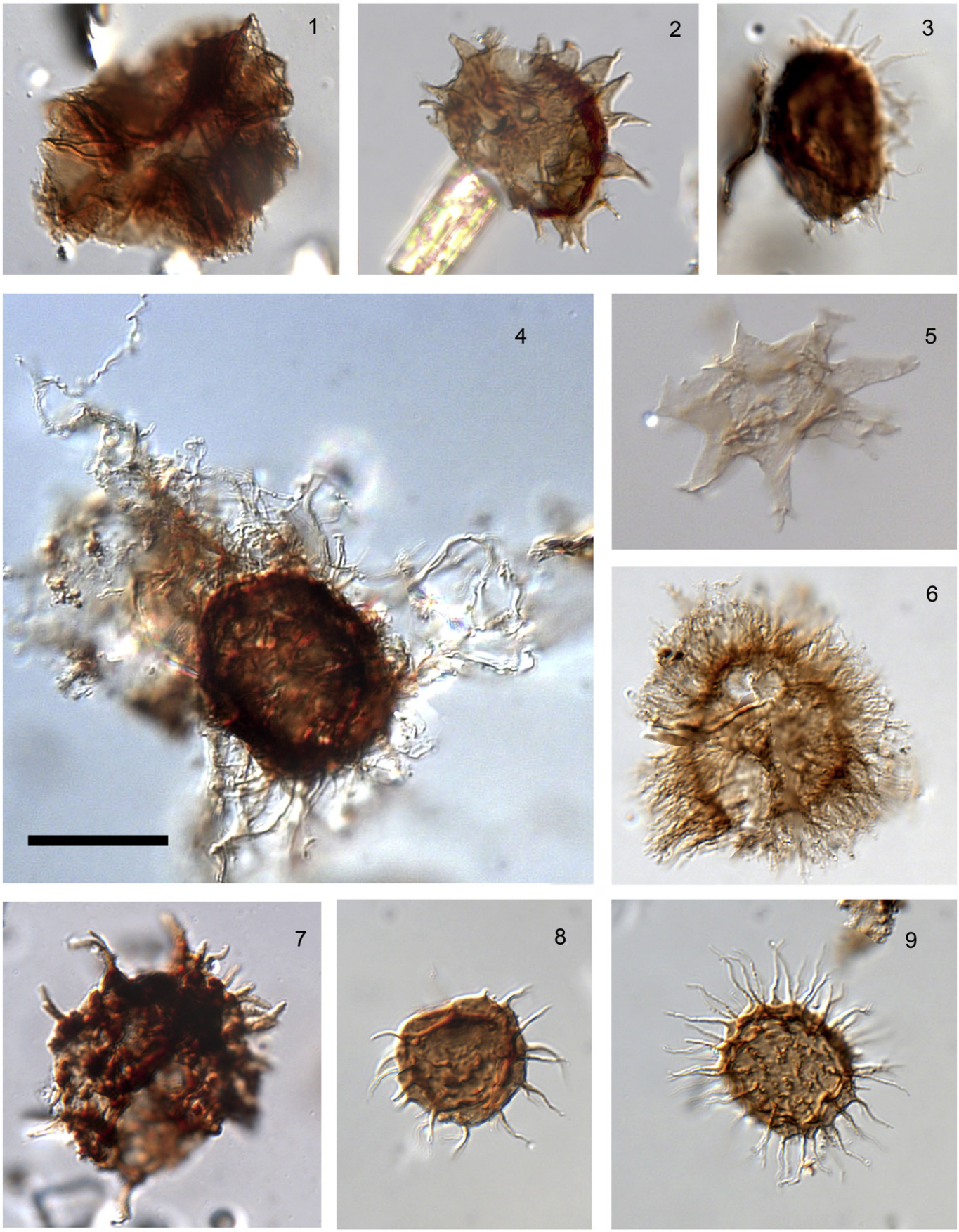
Plate I. Acritarchs from the Oville Formation, Genestosa Member. All the Plates include sample number, slide number, and England finder coordinates for the specimen. Scale bar is equivalent to 20 µm. **(1)** *Liepaina plana* Jankauskas and Volkova in Volkova et al. 1979, PO106-8, UEXP104PO106-8-N, B-28. **(2)** *Polygonium varium* (Volkova 1969) Sarjeant and Stancliffe 1994, PO106-11, UEXP217 PO106-11-N2, S-35. **(3)** *Solisphaeridium implicatum* (Fridrichsone, 1971) Moczydłowska, 1998, PO106-8, UEXP217PO106-8-N1, K-14-2-4. **(4)** *Comasphaeridium longispinosum* Hagenfeldt, 1989, PO106-13, UEXP104PO106-13-N1, S-24-4. **(5)** *Estiastra minima* Volkova 1969, PO106-13, UEXP104PO106-13-N1, M-43. **(6)** *Comasphaeridium silesiense* Moczydłowska, 1998, OV06-2, UEXP104OV06-2a-N1, W-34-4. **(7)** *Solisphaeridium bimodulentum* Moczydłowska, 1998, PO106-8, UEXP104PO106-8-H, Q-33-1. **(8)** *Solisphaeridium flexipilosum* (Slavíková, 1968) Moczydłowska, 1998, AD06-2, UEXP104AD06-2-1, N-27-4. **(9)** *Solisphaeridium multiflexipilosum* (Slavíková, 1968) Moczydłowska, 1998, AD06-2, UEXP104AD06-2-1, M-20-4.

Plate II. Acritarchs from the Oville Formation, Genestosa Member. Scale bar is equivalent to 20 µm. **(1)** *Retisphaeridium dichamerum*, OV06-2, UEXP104OV06-2a-N1,H-39-2-4. **(2, 3)** *Cristallinium cambriense* (Slavíková, 1968) Vanguestaine, 1978. **(2)** Flattened specimen showing rupture into plates along polygonal fields, OV06-2, UEXP104OV06-2a-N1, R-13-2. **(3)** Flattened specimen showing a circular pylome and polygonal fields, AD06-2, UEXP104AD06-2-1, S-33. **(4)** *Protoleiosphaeridium rugulosum* Fombella, 1978, OV09-12, UEXP104OV09-12-1, R-19-3. **(5)** *Acrum radiale* Fombella, 1977, OV09-6, UEXP104OV09-6-1, P-45. **(6)** *Celtiberium dedalinum* Fombella, 1977, OV09-6, UEXP104OV06-2-1, Y-44-3. **(7)** *Abacum normale* Fombella, 1977, specimen showing excystment by median split, AD06-2, UEXP104AD06-2-2, M-36-2. (See on page 84)

Plate III. Acritarchs from the Oville Formation, Genestosa Member. Scale bar is equivalent to 20 µm. **(1, 2)** *Adara alea* Martin in Martin and Dean, 1981. **(1)** OV09-8, UEXP104OV09-8-3, E-32-2-4. **(2)** OV09-8, UEXP104OV09-8-3, N-39-3. **(3, 5)** *Adara matutina* Fombella, 1977. **(3)** OV09-14, UEXP104OV09-14-1, B-32. **(5)** OV09-14, UEXP104OV09-14-1, G-26-2. **(4)** *Celtiberium geminum* Fombella, 1977, OV-09-14, UEXP104OV09-14-1, Z-15-4. **(6)** *Heliosphaeridium lanceolatum* (Vanguestaine 1974) Moczydłowska, 1998, OV09-8 UEXP104OV09-8-3, R-44-3. **(7)** *Multiplicisphaeridium martae* Cramer and Díez, 1972, OV09-14, UEXP104OV09-14-1, L-27-1-2. (See on page 85)

Plate IV. Acritarchs from the Oville Formation, Genestosa Member **(3)**, La Barca Member **(1, 2, 4, 5)**, and Barrios Formation **(6, 7)**. Scale bar is equivalent to 20 µm. **(1, 2)** *Aranidium granulatum* Welsch, 1986. **(1)** Specimen showing circular pylome, BL06-13, UEXP102BL06-13-1, S-19. **(2)** Specimen showing circular pylome. BL06-13, UEXP102BL06-13-1, F-27. **(3)** *Cristallinium ovillense* (Cramer and Díez, 1972) Martin in Martin and Dean, 1981, AD06-1, UEXP104AD06-1-2, J-49. **(4)** *Stelliferidium magnum* Palacios in Palacios *et al.*, 2009, BL06-17, UEXP102BL06-17-2, M-44-4. **(5)** *Timofeevia microretis* Martin in Martin and Dean, 1981, BL06-17, UEXP102BL06-17-2, E-16-2. **(6, 7)** *Timofeevia phosphoritica* Vanguestaine, 1978. **(6)** Specimen showing a polygonal pylome, BL06-24, UEXP102BL06-24-2, S-14. **(7)** BL06-24, UEXP102BL06-24-2, N-40-4. (See on page 86)

Plate V. Acritarchs from the Oville Formation, La Barca Member **(1)**, and Barrios Formation **(2-6)**. Scale bar is equivalent to 20 µm. **(1)** *Cristallinium dubium* Volkova, 1990, BL06-17, UEXP102BL06-17-1, Y-13-1. **(2)** *Leiofusa stoumonensis* Vanguestaine, 1973, UEXP102BL06-26-3, P-36-3. **(3)** *Pirea orbicularis* Volkova, 1990, BL06-26, UEXP102BL06-26-F1, P-38-3-4. **(4, 5)** *Vulcanisphaera turbata* Martin in Martin and Dean, 1981. **(4)** BL06-26, UEXP102BL06-26-3, C-25. **(5)** BL06-26, UEXP102BL06-26-4, P-45-4. **(6)** *Stelliferidium cortinulum* (Deunff 1961) Deunff, Gorka and Rauscher 1974, BL06-26, UEXP102BL06-26-F1, Q-20-3. (See on page 87)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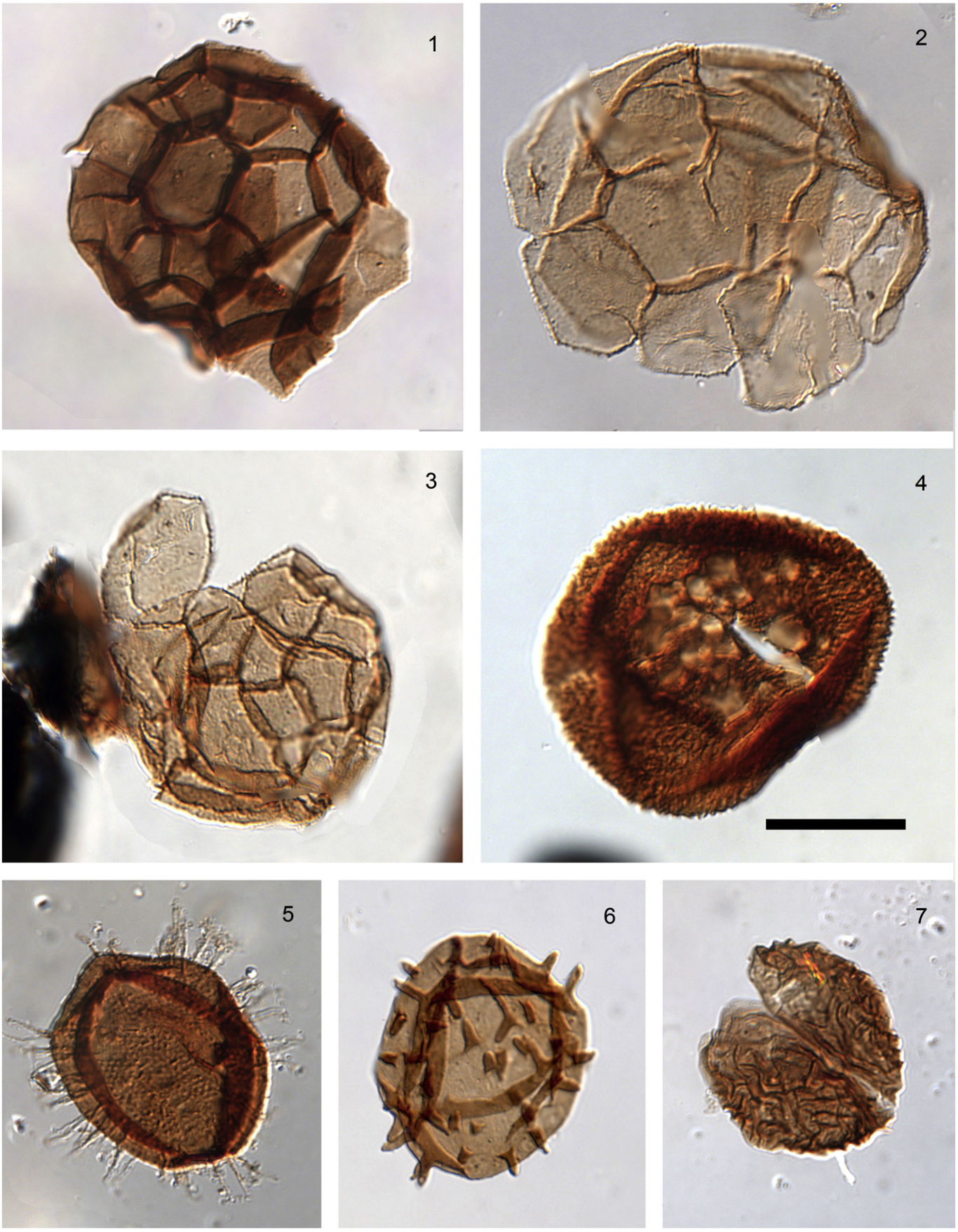


Plate II. *(Caption on page 82).*

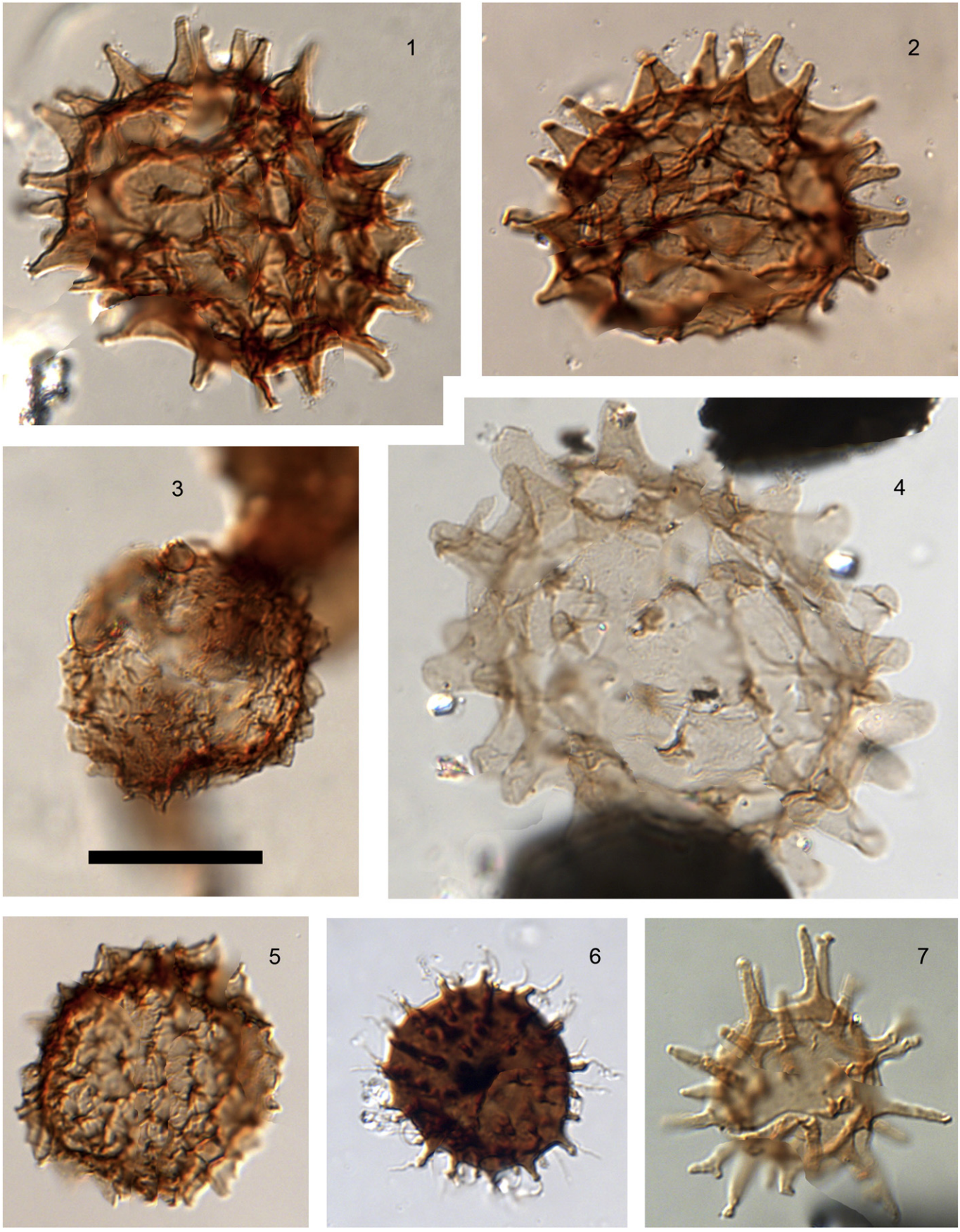


Plate III. *(Caption on page 82).*

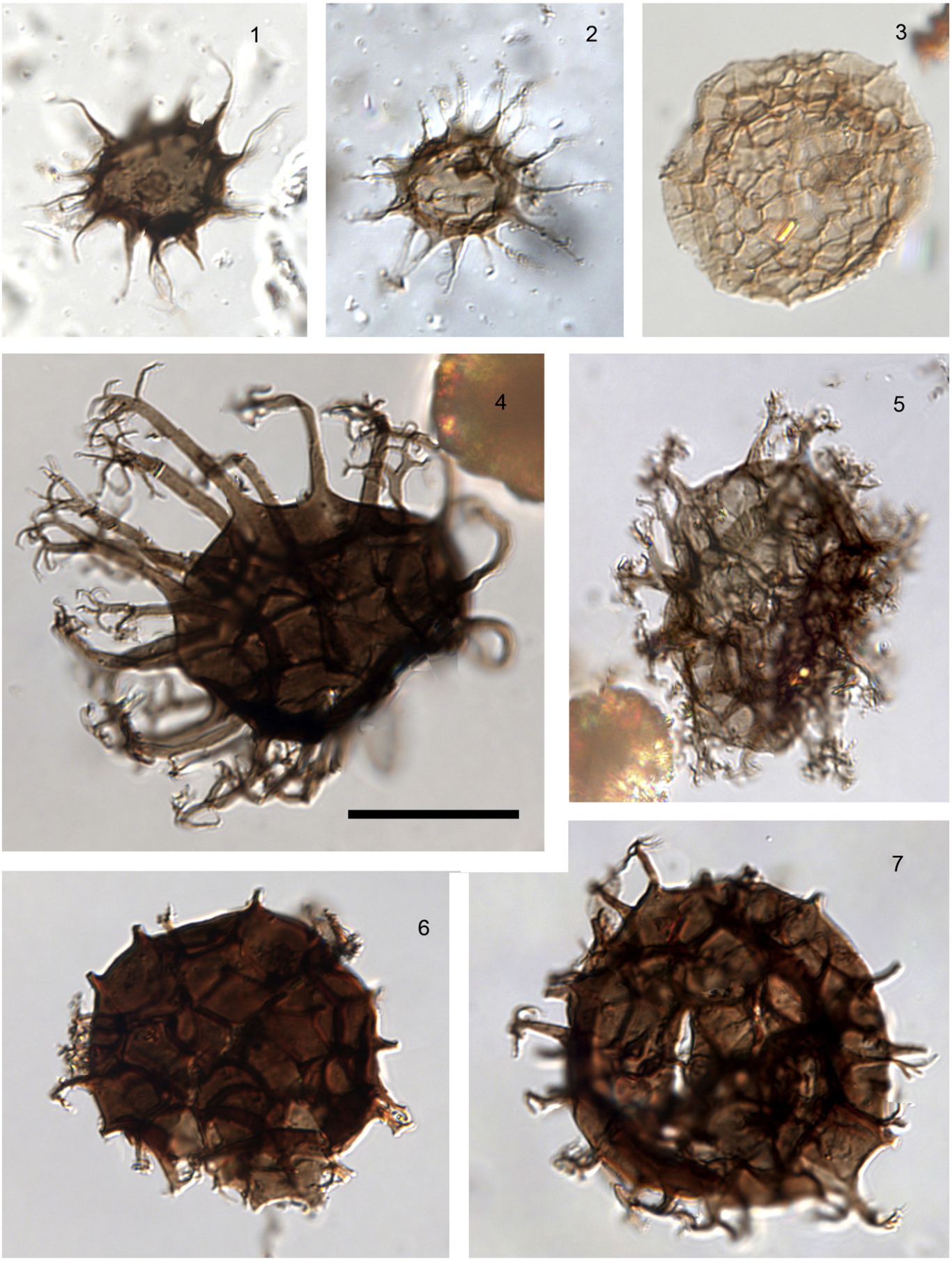


Plate IV. *(Caption on page 82).*

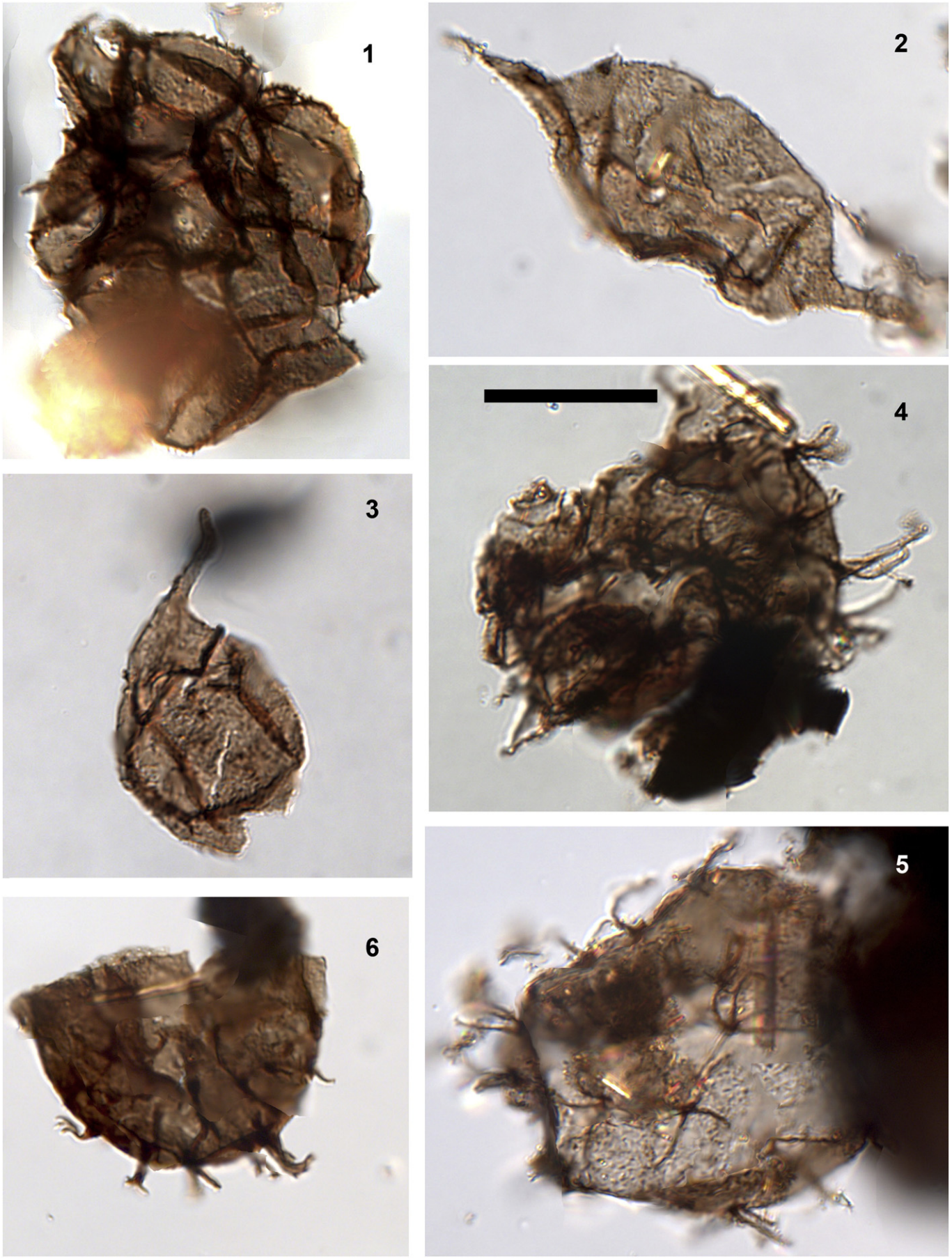


Plate V. *(Caption on page 82).*

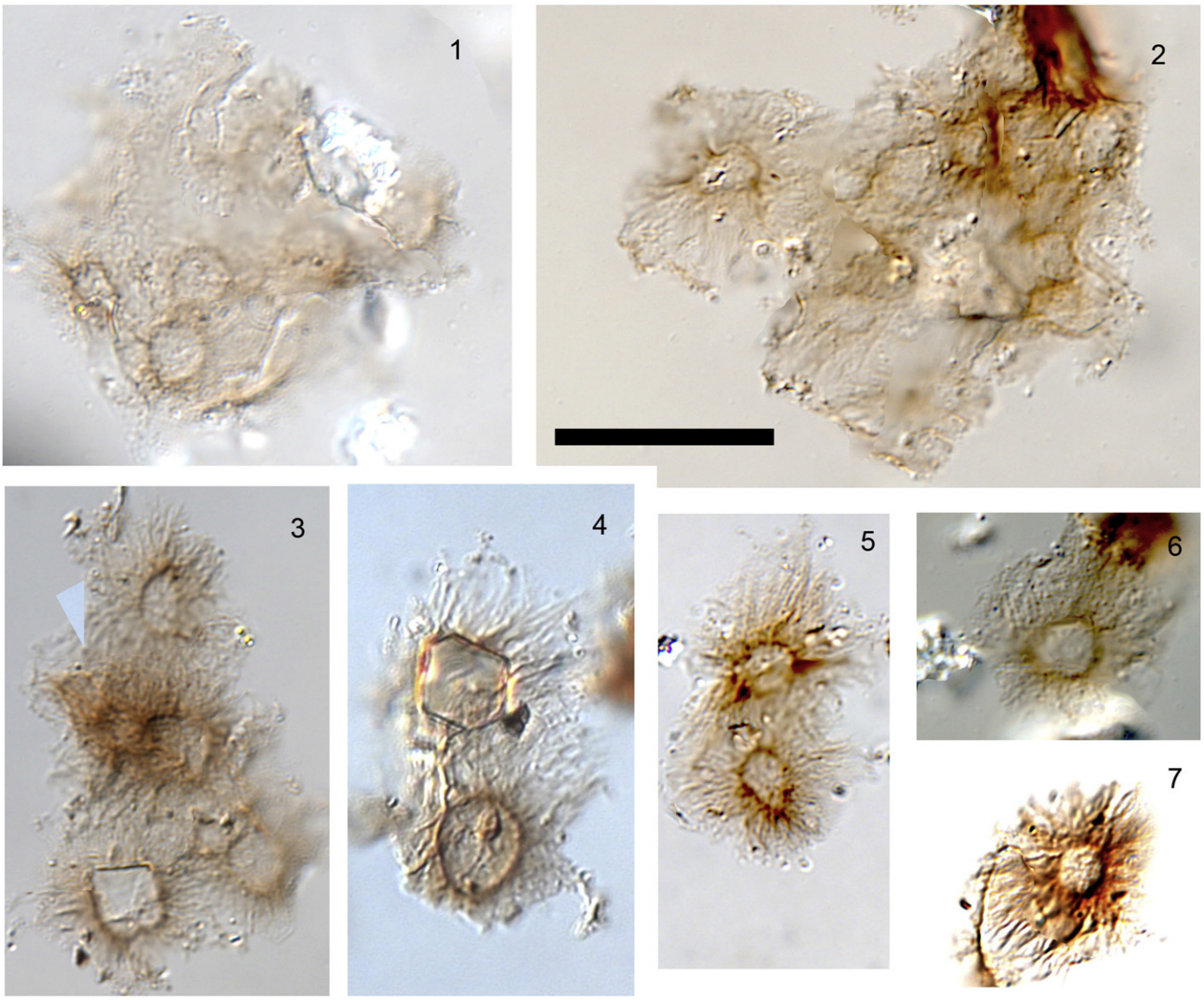


Plate VI. (1-6) *Comasphaeridium francinae* Jachowicz-Zdanowska, 2013. Specimens displaying dimensional variability and preservational states. **(1, 2)** Cluster of mucilaginous aspect, inside which is starting the individualization of the specimens and the development of processes. **(1)** PO106-8, UEXP104PO106-8-H, Z-44-4. **(2)** PO106-8, UEXP104PO106-8-H, E-23-3. **(3-5)** Cluster with individualized specimens. **(3)** PO106-13, UEXP104PO106-13-N1, M-44. **(4)** Vesicle of one of the specimens is distorted by pyrite pseudomorph, PO106-13, UEXP104PO106-13-N1, U-38. **(5)** PO106-8, UEXP104PO106-8-No-2, Q-46-3-3. **(6)** PO106- 6, UEXP104PO106-8-H, B-33-3. **(7)** PO106-11, UEXP104PO106-11-N2, U-17-1-3. Scale bar is equivalent to 20 μm.

Canada, Cambrian Stage 5 to the lowermost Drumian *Paradoxides eteminicus* Zone and *P. hicksii* Zone, Chamberlains Brook Formation and the lower part of the Manuels River Formation, eastern Newfoundland (Martin and Dean, 1984, 1988); Dugald and Gregwa Formations, Cape Breton Island, Nova Scotia (Palacios et al., 2012b); and Forest Hills Formation (Fossil Brook Member) in New Brunswick (Palacios et al., 2012a). Wales, in the Nant-y-big Formation on the St. Tudwal's Peninsula (Young et al., 1994) in beds attributed to the *Tomagnostus fissus* Zone (equivalent to the *hicksii* Zone, Fletcher, 2007). Poland, Sosnowiec Formation in beds assigned to *Acadoparadoxides oelandicus* and *Paradoxides paradoxissimus* zones (Jachowicz-Zdanowska, 2013).

Comasphaeridium maximum sp. nov. (Plate VII, 1–4)

1979 *Comasphaeridium piliferum* Fombella, Lámina IV, 66; Lámina V, 80 (nomen nudum)

2008 *Baltisphaeridium pseudofaveolatum* Fridrichsone–Palacios Fig. 3L

Holotype: Sample OV09-11, UEXP104OV09-11-2 England finder coordinates E-36-1 Plate VII, 1.

Type locality: Oville section, Oville, Leon Province Fig. 1 (UTM data zone ED50 30871069, 475327237).

Type stratum: Alternations of mudstones and nodular limestones, bottom of Oville Formation (Genestosa Member).

Etymology: Latin, *maximus*, with reference to large dimensions.

Diagnosis: Large vesicle circular to oval in outline, originally spherical and occasionally wrinkled due to compression; surface spongy, bearing solid and flexible hair-like processes densely packed that frequently coalesce distally, presenting in the basal part of the process a trabecular appearance.

Dimensions: Vesicle width 50–95 μm (mean 71 μm). Process length 8–18 μm (mean 13 μm). (Based on 18 well preserved specimens.)

Dimension holotype: Vesicle width 60 μm. Process length 15 μm.

Discussion: Based on 25 specimens. Large *Comasphaeridium*, reaching 90 μm vesicle diameter. Process length ranges from 15–25% of vesicle diameter, 25% in the holotype. In the larger specimens, the processes are relatively shorter, about 15% of vesicle diameter. Processes are solid, wider at the base, where their width ranges from 0.6 to 1.4 μm. The

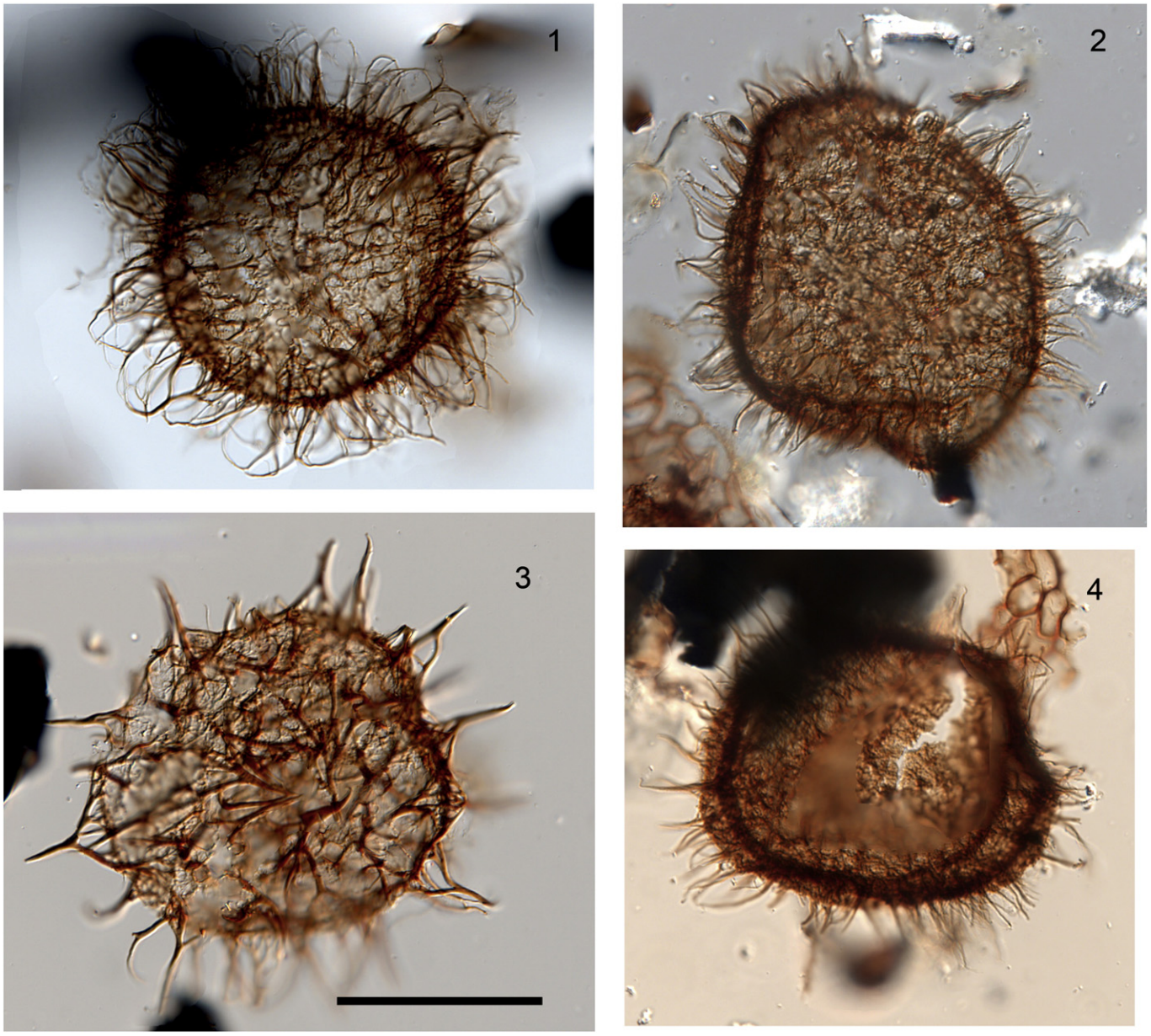


Plate VII. (1-4) *Comasphaeridium maximum* sp. nov. **(1)** Holotype, vesicle with spongy surface bearing solid and flexible hair-like processes that coalesce distally. OV09-11, UEXP104OV09-11-2, E-36-1. **(2, 4)** Specimens with vesicle of large dimensions and relatively short processes. **(2)** OV06-3, UEXP104OV06-3, V-28. **(4)** OV06-3, UEXP104OV06-3, U-39-1-3. **(3)** Specimen with processes coalescent in distal part, showing in basal part a trabecular appearance, OV09-11, UEXP104OV09-11-4, X-15-4. Scale bar is equivalent to 40 μm.

distance between the processes ranges between 0.8 and 2 μm. The processes are very flexible and usually attach distally showing a trabecular appearance (Plate VII, 1–3).

Comparison: Fombella (1979) illustrates material of this form as *C. piliferum* sp. nov., although she did not provide a formal description, and it therefore has been considered a nomen nudum (Fensome et al., 1990). Two of the largest Paleozoic species of *Comasphaeridium* have been described from the lower Cambrian and the Ordovician. The lower Cambrian *C. molliculum* Moczydłowska and Vidal, 1988, which may reach 60 μm, has denser, finer, and shorter processes, and the lower Ordovician *C. tonsum* Cramer and Díez, 1977, which is smaller (up to 50 μm), has processes similar to those of *C. maximum*, but less densely spaced and does not have a spongy surface.

Stratigraphic occurrence: Oville Formation (Genestosa Member) middle Cambrian (Drumian), IMC2-IMC4 zones, with maximum abundance in the IMC3 Zone.

Genus ***Eliasum*** Fombella, 1977 emend.

Type species: *Eliasum llaniscum* Fombella, 1977.

Original diagnosis (Fombella, 1977, p. 118): Vesícula elongada, subprismática, con polos redondeados y membrana delgada. Constituido por cinco o seis aristas longitudinales que se disponen de manera regular y equidistalmente. Estas pueden ser lisas u ornamentadas por pequeñas espinas, dentículos o elementos similares. Las costillas están bien definidas y a menudo acentuadas por pliegues secundarios. También pueden ser almenados, llevando una o más hileras de elementos denticulados. Las áreas intercostales pueden ser lisas u ornamentadas por una escultura de tamaño menor que la de las aristas. La vesícula tiende a fracturarse a lo largo de las costillas, que demuestran ser zonas estructuralmente débiles.

Translation of the original diagnosis (Cramer and Díez, 1979, p. 78): Thin-walled, elongate, subprismatic vesicles with rounded poles, formed by five or six regularly and equidistantly arranged longitudinal arists. These arists may be smooth or ornamented by small spines, denticules or similar elements. The ribs are sharply defined and are often

accompanied by secondary folds. They may also be almenate, bearing one or more rows of denticulate elements. The intercostal areas may be smooth or ornamented by a sculpture which is of smaller size than of the arists. The vesicle tends to split along one of the ribs which are structurally weak zone.

Emended diagnosis: Vesicle originally ellipsoidal, flexible and because of deformation often fusiform, but also with a spherical or polygonal outline. The vesicle is divided into elongate areas or plates* whose suture zones may be smooth or ornamented by small denticules, granules, or short conical processes. Surface psilate to granulate. Excystment by polar opening of the plates along the lines of suture.

Discussion: The emended diagnosis is based on new material from the type area (Oville section, Fig. 3) that includes abundant and well preserved specimens of *Eliasum llaniscum*, *E. asturicum*, and *E. fombellae* sp. nov., and scarcer *E. pisciforme*. The material from the Adrados and Barrios de Luna sections (Figs. 5–7) includes only *E. llaniscum*.

The excellent preservation of the material makes it possible to identify a range of morphologies of *Eliasum* that result from taphonomic processes. These morphologies can lead to confusion with other genera (for example, *Leiosphaeridia*, *Cristallinium*, *Retisphaeridium*). The flexibility of the vesicle allows different shapes to result by flattening, most evident in *E. asturicum* and *E. fombellae* sp. nov. (Plate VIII, 5–7, 10, 13–16), where the ornamentation of the suture lines is a referent for analysis. The commonest morphology in *Eliasum* is the fusiform (Plate VIII, 1–4, 8, 9, 12), since the stablest position is when the major axis is horizontal. In this case, during compaction of the sediment, the flattening is in the direction of the minor axis, and the folds are concentrated along the suture lines to become areas of weakness. In the case of spherical or polygonal morphologies, the flattening occurs in the direction of the major axis (Plate VIII, 7, 10, 14–16). Between these extremes there is a full spectrum of intermediate morphologies. This taphonomic process can lead to confusion with other acritarchs with similar sutural ornamentation: *Eliasum llaniscum* with *Retisphaeridium dichamerum*, *E. asturicum* with *C. cambriense*, and *E. fombellae* with *Cristallinium dubium or C. randomense*, particularly when based on scarce and poorly preserved material. Also, flattened specimens of large *Leiosphaeridia* can be confused with *Eliasum llaniscum* when the excystment along the lines of suture is not present. The above must be carefully considered in the use of *Eliasum* chronostratigraphically. The type of excystment of *Eliasum*, suggested in the original diagnosis (Fombella, 1977, p. 118), has been described in the Ediacaran genus *Calyxia* (Willman and Moczydłowska, 2008).

Eliasum fombellae sp. nov. (Plate VIII, 8–16).

1981 *Eliasum* cf. *E. asturicum* Martin in Martin & Dean, Plate 2, 6

1988 *Eliasum* cf. *E. asturicum* Martin in Martin & Dean – Martin & Dean Plate 15, 3

1993 *Eliasum asturicum* Fombella – Fombella et al., Plate 1, 2

Holotype: Sample OV09-8, UEXP104 OV09-8-3, England finder coordinates J-20-4, Plate VIII, 8.

Paratype: Sample OV09-8, UEXP104 OV09-8-1 England finder coordinates Z-35-2 Plate VIII, 9.

Type locality: Oville section, Oville, Leon Province Fig. 1 (UTM data zone ED50 30875667, 475331433).

Type stratum: Upper part of alternations of mudstones and nodular limestone siltstone of Oville Formation (Genestosa Member).

Etymology: Dedicated to Dr María Amor Fombella, a pioneer in acritarch studies of Oville Formation.

Diagnosis: Vesicle originally ellipsoidal, very flexible that grades in flattened specimens to forms mainly fusiform, but also spherical and polygonal outlines. The vesicle is divided into spindle-shaped areas or plates, and their sutures, usually folded, are ornamented with small homomorphic conical processes with a flexible filiform distal part. Vesicle surface smooth. Excystment by polar opening of the plates along the suture lines.

Dimensions: Length 47–84 μm (mean 64 μm), width 27–49 μm (mean 34 μm), length width ratio 0.38–0.73 (mean 0.54). Length of sutural processes 1.2–2.2 μm (mean 1.65 μm), number of ornamented sutures 5–8 (mean 6). Based on 60 well preserved ellipsoidal and fusiform flattened specimens. Measurements made on 43 specimens in which the original size of the vesicle is reconstructed by deploying the folds in the equatorial area (Fig. 10) (width of the fold + width of collapsed vesicle) are: length 49–84 μm (mean 64 μm), width 40–61 μm (mean 50 μm), length–width ratio 0.61–0.9 (mean 0.78).

Dimensions of holotype: Length 62 μm, width 29, length–width ratio 0.48; width of the folds + width of collapsed vesicle 48 μm, length width ratio 0.78 (Fig. 10).

Discussion: Based on observations on more than five hundred specimens. The vesicle originally ellipsoidal and usually flattened gives fusiform forms, but also spherical and polygonal (see above discussion of genus *Eliasum*). Reconstruction of the original shape was based on ellipsoidal and fusiform specimens, in which the flattening is limited to longitudinal folds that present their greatest width in the equatorial plane. The unfolding was made at the equator (Fig. 10).

Comparison: *Eliasum fombellae* is similar to *Eliasum asturicum* Fombella, 1977 in having regularly distributed ornamental elements in the interplate ridges. *Eliasum asturicum* have small denticules (Plate VIII, 3–7), and *Eliasum fombellae* have shorter solid processes with a conical base (Plate VIII, 8–16). The vesicle surface of *E. fombellae* is smooth, and that of *E. asturicum* smooth to microgranulate (Plate VIII, 3–7).

Stratigraphic occurrence: Oville Formation (Fig. 4) middle Cambrian (Drumian), IMC3 Zone. Manuels River Formation at Manuels River, eastern Newfoundland, *Adara alea* Zone Martin and Dean, 1988.

Genus ***Symplassosphaeridium*** Timofeev 1959.

Type species: *Symplassosphaeridium tumidulum* Timofeev 1959.

Symplassosphaeridium cambriense Slaviková 1968, emended (Plate IX, 1–4)

Synonymy:

1968 *Symplassosphaeridium cambriense* Slaviková sp. nov. – Slaviková, Plate II, 4,6

1981 *Symplassosphaeridium* cf. *cambriense* Slaviková – Erkmen & Bozdoğan, Plate 2, 6, 7.

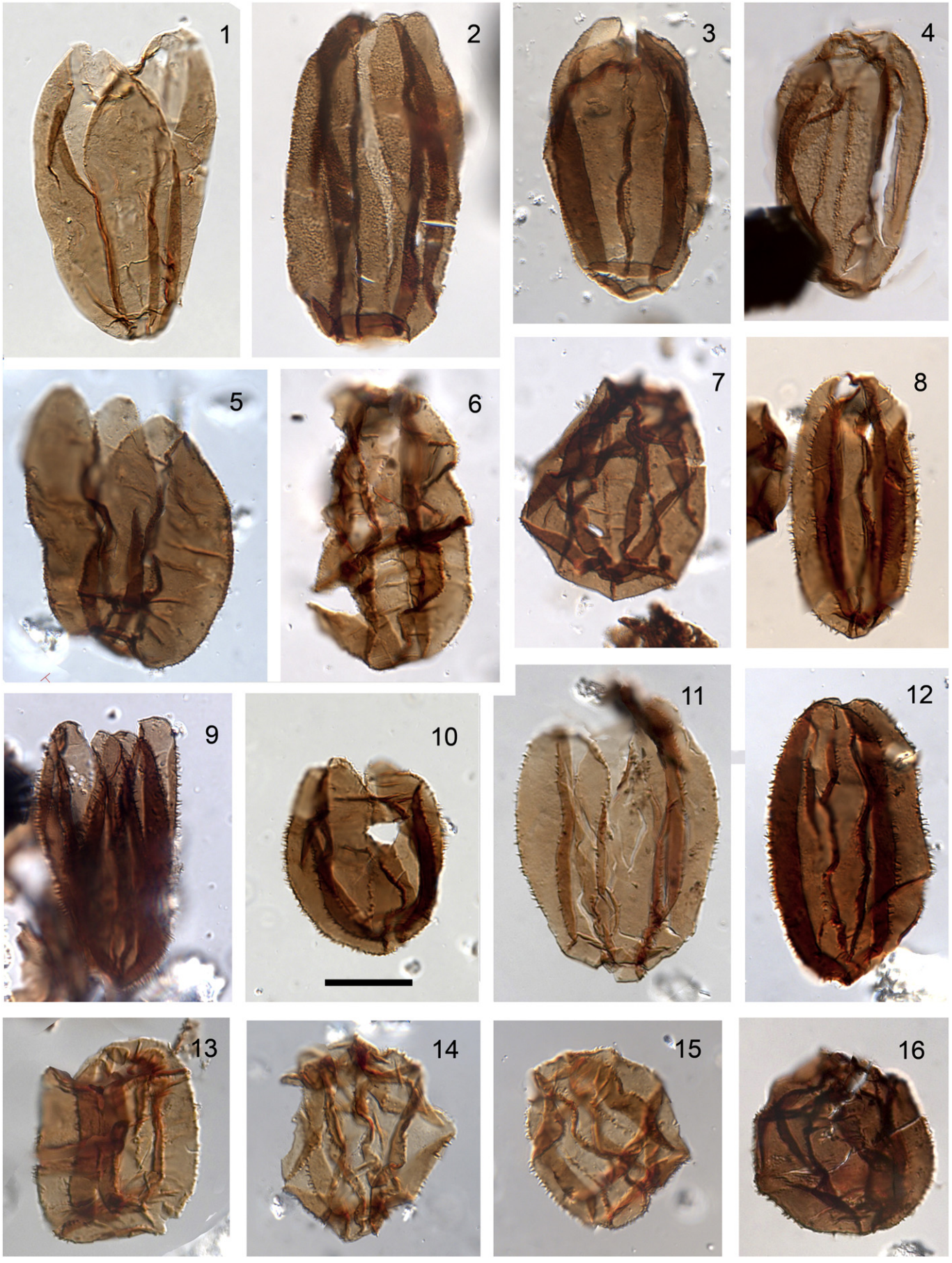
1991 Coenobial acritarchs Di Millia, Plate 1, Figs. 1–3

1997 Coenobial acritarchs Di Millia – Dean et al., Fig. 8, V

2009 *Symplassosphaeridium cambriense* Slaviková – Palacios et al., Fig. 5 A

2012b *Symplassosphaeridium cambriense* Slaviková – Palacios et al., Fig. 10 A, B

Plate VIII. Acritarchs from the Oville Formation, Genestosa Member. A representative collection of *Eliasum* species displaying different preservational stages. **(1)** *Eliasum llaniscum* Fombella, 1977, specimen showing excystment by polar opening of the plates along the lines of suture, AD06-2, UEXP104AD06-2-2; O-24-3. **(2)** *Eliasum pisiformis* Fombella, 1977, fusiform specimen showing a granulate surface ornamentation and incipient excystment by polar opening of the plates along the suture lines, OV06-2, UEXP104OV06-2-1, Z-44-1-2. **(3-7)** *Eliasum asturicum* Fombella, 1977. **(3, 4)** Fusiform specimen showing diagnostic granulate ornamentation along the suture lines **(3)** OV06-2, UEXP104OV06-2a-1; E-39-4. **(4)** OV09-6, UEXP104OV09-6-2; Z-44-3. **(5)** Specimen showing excystment by polar opening of the plates along the lines of suture UEXP104OV06-2a-1; K-36. **(6)** Specimen showing flattening in the direction of both minor and major axis, OV06-2, UEXP104OV06-2a-1; J-19. **(7)** Flattened specimen showing a polygonal morphologies, OV06-2, UEXP104OV06-2a-1; J-27. **(8–15)** *Eliasum fombellae* sp. nov. **(8)** Holotype, fusiform specimen showing longitudinal folds and typical sutural processes, OV09-8, UEXP104OV09-8-3; J-20-4. **(9)** Paratype, showing excystment by polar opening of the plates along the suture lines, OV09-8, UEXP104OV09-8-1; Z-35-2. **(10, 16)** flattening specimens showing spherical morphologies. **(10)** OV09-8, UEXP104OV08-1; N-50-4. **(16)** OV06-3, UEXP104OV06-3 N; K-32-1. **(11, 12)** Flattened specimens showing ellipsoidal morphologies. **(11)** OV06-3, UEXP104OV06-3 N; B-22-1. **(12)** OV09-8, UEXP104OV09-8-3; G-30-4. **(13–15)** Flattened specimens showing polygonal morphologies. **(13)** OV03-3, UEXP104OV06-3 N; C-17-3. **(14)** OV09-10, UEXP104OV09-10-3; E-31. **(15)** OV09-10, UEXP104OV09-10-3; P-25-4.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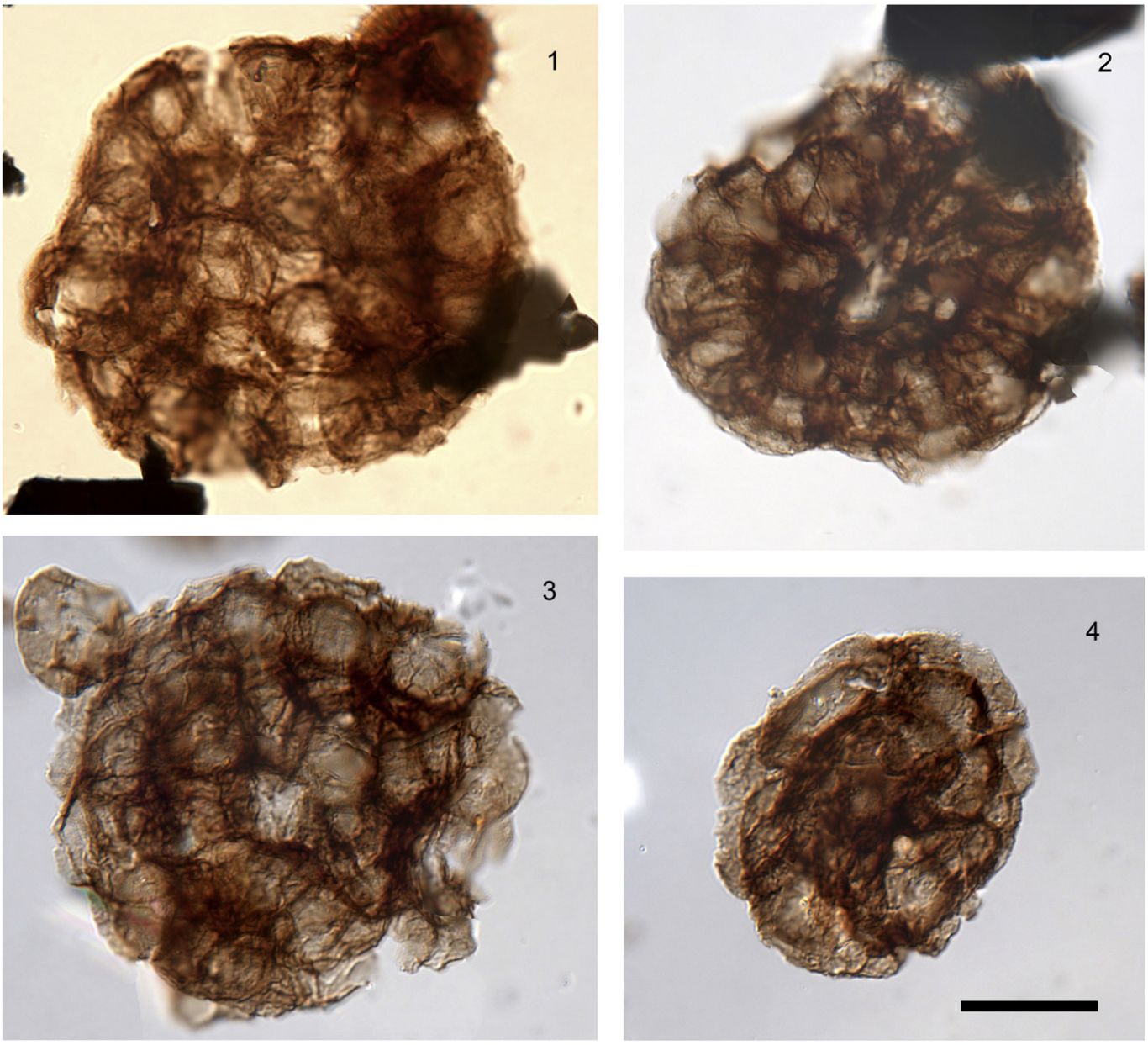


Plate IX. (1–4) *Symplassosphaeridium cambriense* Slavíková, 1968, emend., specimens showing a variable number of spherical vesicles arranged with a planispiral coiling. Scale bar is equivalent to 20 μm. **(1)** AD06-2, UEXP104AD06-2-2; D-19-1-3. **(2)** AD06-2, UEXP104AD06-2-1; F-18. **(3)** UEXP104AD06-2-1; J-37-3-4. **(4)** UEXP104AD06-2-2; E-31-3.

2012 *Symplassosphaeridium cambriense* Slaviková – White et al., Fig. 8 A

Original diagnosis: Spherical cluster consist of spherical vesicles. The single spherical vesicles of different size ranging from 4–9 μm. They overlap one another, in cluster ± 10 vesicles. Their surface firm, translucent, smooth, very thin (Slavíková, 1968, p. 202).

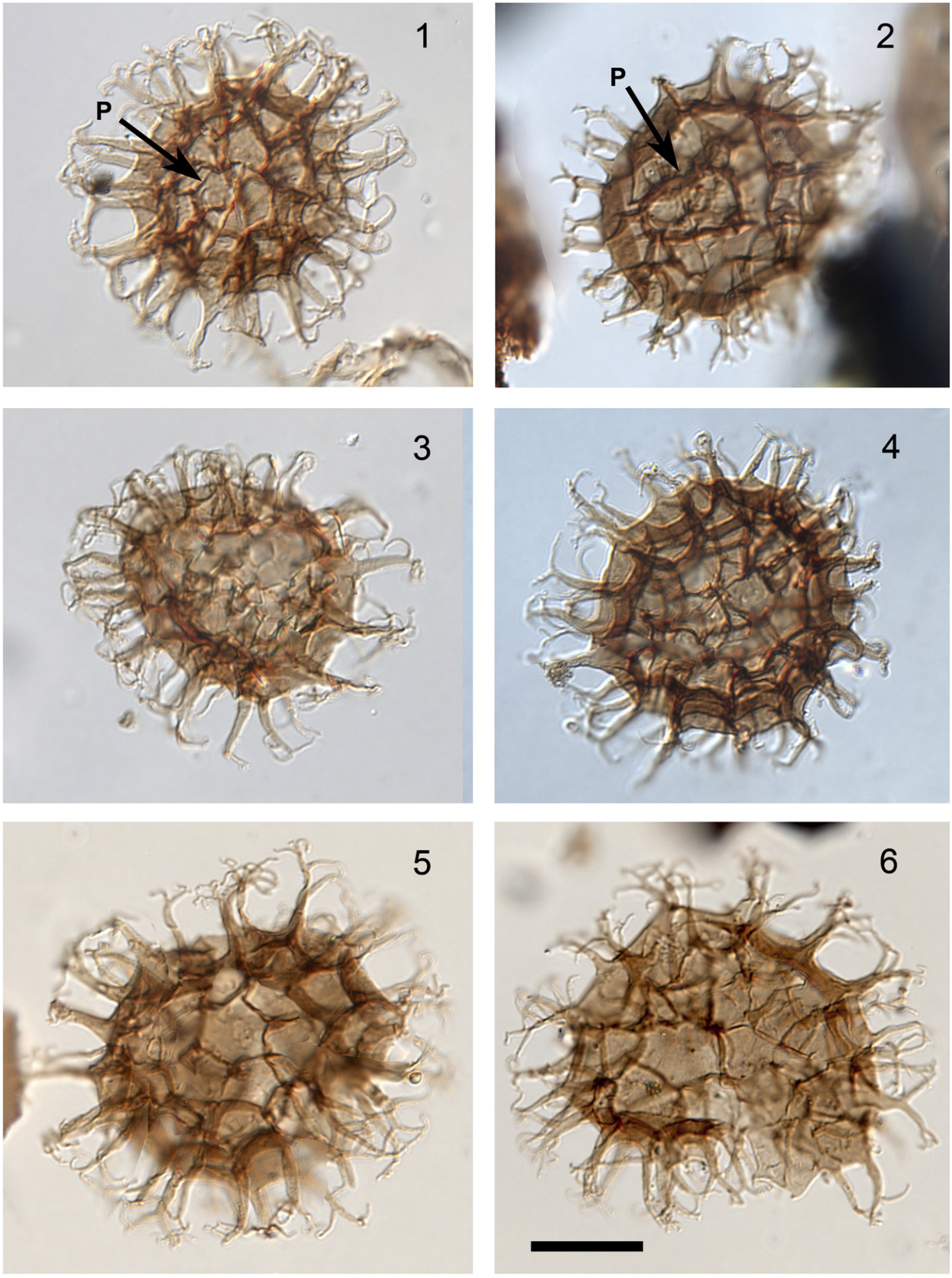
Emended diagnosis: Spherical cluster of a variable number of soldered spherical vesicles, that overlap one another following the pattern of a planispiral coiling. The vesicles are enveloped by a sort of mucilage and their size grow from the centre to the periphery.

Dimensions: Total diameter of cluster 27–93 μm (mean 51 μm). Diameter of individual vesicles: maximum 7–27 μm (mean 14 μm), minimum (3–17 μm) (mean 6 μm). Number of individual vesicles of the cluster 5–54 (mean 20). Based on 94 specimens.

Discussion: The greater variability seen in the material from the Oville Formation is the basis for the emended diagnosis of *S. cambriense*. The material from the Oville Formation conforms well to the type material of *Symplassosphaeridium cambriense* from the middle Cambrian of the Czech Republic (Slavíková, 1968) and coenobial acritarch sensu Di Millia, 1991, but presents a greater variability than that seen in the forms described by Slavíková (1968) and Di Millia (1991).

Stratigraphic occurrence: This species has been widely recorded from the upper middle Cambrian–lowermost Furongian of peri-Gondwanan terranes. Slavíková (1968) erected this species based on material from the

Plate X. (1–6) *Timofeevia densa* sp. nov. **(1)** Holotype, specimen showing a circular pylome (black arrow), AD06-2, UEXP104AD06-2-1; T-25-4. **(2)** Specimen showing a deformed circular pylome (black arrow), AD06-2, UEXP104AD06-2-1; Y-45. **(3)** AD06-2, UEXP104AD06-2-1; H-36-3-4. **(4)** AD06-2, UEXP104AD06-2-2; D-30-1. **(5)** AD06-2, UEXP104AD06-2-1; M-36. **(6)** AD06-2, UEXP104AD06-2-1; K-44-1-2. Scale bar is equivalent to 20 μm.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middle Cambrian Jince Formation of the Czech Republic in levels assigned to the *Ellipsocephalus hoffi* sub-Zone or the *Ellipsocephalus hoffi–Rejkocephalus* Abundance Zone sensu Fatka (2006), correlated with the Upper Languedocian (Álvaro et al., 2004). Di Millia (1991) reported it as a coenobial acritarch in the Upper Cambrian (age defined on acritarchs) Solanas Formation of Sardinia. In Nova Scotia, Cape Breton Island, it occurs in the Mira River area in an interval that contains *Paradoxides davidis* (Palacios et al., 2009) and extends to the lower Furongian (T. Palacios, unpublished data), and in the Bourinot belt it occurs in the MacMullin Formation (Palacios et al., 2012b), where it occurs with *Tubulosphaera craterae* sp. nov. In Nova Scotia, in the Meguma group, White et al. (2012) reported *S. cambriense* in the Tupper Lake Brook Formation. Erkmen and Bozdogan (1981) reported *Symplassosphaeridium* cf. *cambriense* from the Sosink Formation, Turkey and, from the same formation, Dean et al. (1997) reported coenobial acritarchs in levels with *Solenopleuropsis* sp., of the upper part of the *P. paradoxissimus* Zone sensu Dean (2005). In Spain, Palacios (1997) reported this species (as coenobial acritarchs) from the Acón Group of the Celtiberian Chains, assigned to the Languedocian. In the Oville Formation (the Barrios de Luna and Adrados sections), its lowest occurrence is bracketed between the *Solenopleuropsis marginata* Zone and levels with *Paradoxides* cf. *davidis* (lower Languedocian), and it extends into the IMC6 Zone.

Genus ***Timofeevia*** Vanguestaine1978

Type species: *Timofeevia lancarae* (Cramer and Díez, 1972) Vanguestaine, 1978, p. 272 (= *Multiplicisphaeridium lancarae* Cramer and Díez, 1972, p. 42, Plate 1:1–4, 6, 8), Spain, the Cantabrian Mountains at Láncara de Luna, upper middle Cambrian.

Original Diagnosis (Vanguestaine, 1978): Coque creuse, polyédrique, constituée d'un agencement de facettes polygonales. Selon le nombre de facettes, le contour de la coque est polygonal ou arroundi. Membrane mince, apparemment composée d'une seule couche. Les facettes sont délimitées par des sutures épaissies, parfois proéminentes en forme de crêtes membraneuses. Souvent, elles sont incurvées vers l'intérieur de la coque. Appendices simples, bifurqués ou ramifiés, creux ou partiellement creux et communiquant librement avec la cavité centrale de la coque. Ils sont portés par les sutures des facettes, distribués sur ces dernières ou confinés à leur point de convergence. Membrane lisse, chagrinée, microgranulée ou microrugulée, Structure de déhiscence apparemment constituée parla perte d'un nombre variable de facettes polygonales (Vanguestaine, 1978, p. 272).

English translation (Cramer and Díez, 1979): Hollow, polyhedrical vesicle formed by an arrangement of polygonal plates. According to the number of plates, the outline of vesicle is polygonal or rounded. The vesicle wall is thin and is apparently single-layered. The plates are bordered by thickened sutures which may be elevated so as to form membranous crests. These crests are often curved towards the interior of the vesicle. The processes are simple, bifurcated or ramified, hollow or partially hollow and freely communicating with the central body cavity. They may emplaced on the sutures, may be distributed over the plates or may be restricted to the points of convergence of the sutures. The vesicle wall is smooth, chagreenate, microgranulate, or microrugulate. The dehiscence structure is apparently formed by the loss of a variable number of polygonal plates.

Remarks: Although Vanguestaine (1978) described the genus *Timofeevia* mainly based on characters of material of *Timofeevia phosphoritica* Vanguestaine, 1978, from the Grand-Halleux borehole, Stavelot Massif, he selected *Multiplicisphaeridium lancarae* Cramer and Díez, 1972, from the Oville Formation in Láncara de Luna as the type species. The abundant material of *T. lancarae* from the Oville Formation in the Barrios de Luna and Adrados sections examined here (Figs. 4–5) present important differences in significant diagnostic characters which do not conform to the original description of the genus *Timofeevia*. The type of pylome (although a small number of specimens) is circular in *T. lancarae* (Moczydłowska et al., 2011, Fig. 3B, C; and Plate XII, 2, 6) and the new species *T. densa* and *T. heteromorpha* This contrast to Vanguestaine's original diagnosis when the excysyment results from the loss of a variable number of polygonal plates. In *T. lancarae*, the sutures of the plates do not have membranous crests, but rather folds due to the collapse of the vesicle, according to *M. lancarae*'s original description (Cramer and Díez, 1972, p. 42). Another important diagnostic character of *Timofeevia* is the type of the processes, which are conical or tapering in the type species.

Other species of *Timofeevia* such as *T. phosphoritica* and *T. pentagonalis* show important morphological differences (Palacios unpublished observation) and include forms with a polygonal (heptagonal) pylome, thick polyhedral vesicle formed by the arrangement of easily disarticulated polygonal plates, and mainly tubular processes. The characters *T. phosphoritica* and *T. pentagonalis* are intermediate between *Timofeevia* and *Stelliferidium magnum* and *S. albani* (Palacios in Palacios et al., 2009), sharing with these last the presence of a heptagonal pylome, clear plate rupture and mainly tubular processes. The stratigraphic distribution of these species is mainly Upper Drumian–Furongian (IMC6 and Furongian) or the A2 Zone of Martin and Dean, 1988 to Furongian.

Timofeevia densa sp. nov. (Plate X, 1–6)

1991 *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Albani et al., Plate 2, 8, 9; Plate 3, 11

2012b *Timofeevia* sp. B – Palacios et al., Fig. 9, E–F

Holotype: Sample OV09-11, UEXP104OV09-11-3, England finder coordinates S-37, Plate X, 1.

Type Locality: Adrados section, Oville Formation (Genestosa Member), Leon Province Fig. 1 (UTM (ED50) 314805, 4749311).

Type stratum: Oville Formation, mudstones of the upper part of the Genestosa Member (Fig. 2).

Etymology: From Latin *densa*, in reference to the numerous and densely arranged processes.

Diagnosis: Spherical to polygonal vesicle with thin wall, bearing conical or distally tapering homomorphic hollow processes, ramified up to the third order. Depending on the development of the cyst, the outline of the vesicle is polygonal or rounded, and the vesicle shape grades from spherical to divided into polygonal areas (plates) limited by ridges or lines of weaknesses, usually folded, that connect the bases of the processes, located at the points of convergence of the plates. The vesicle wall is psilate with excystment in form of a circular pylome.

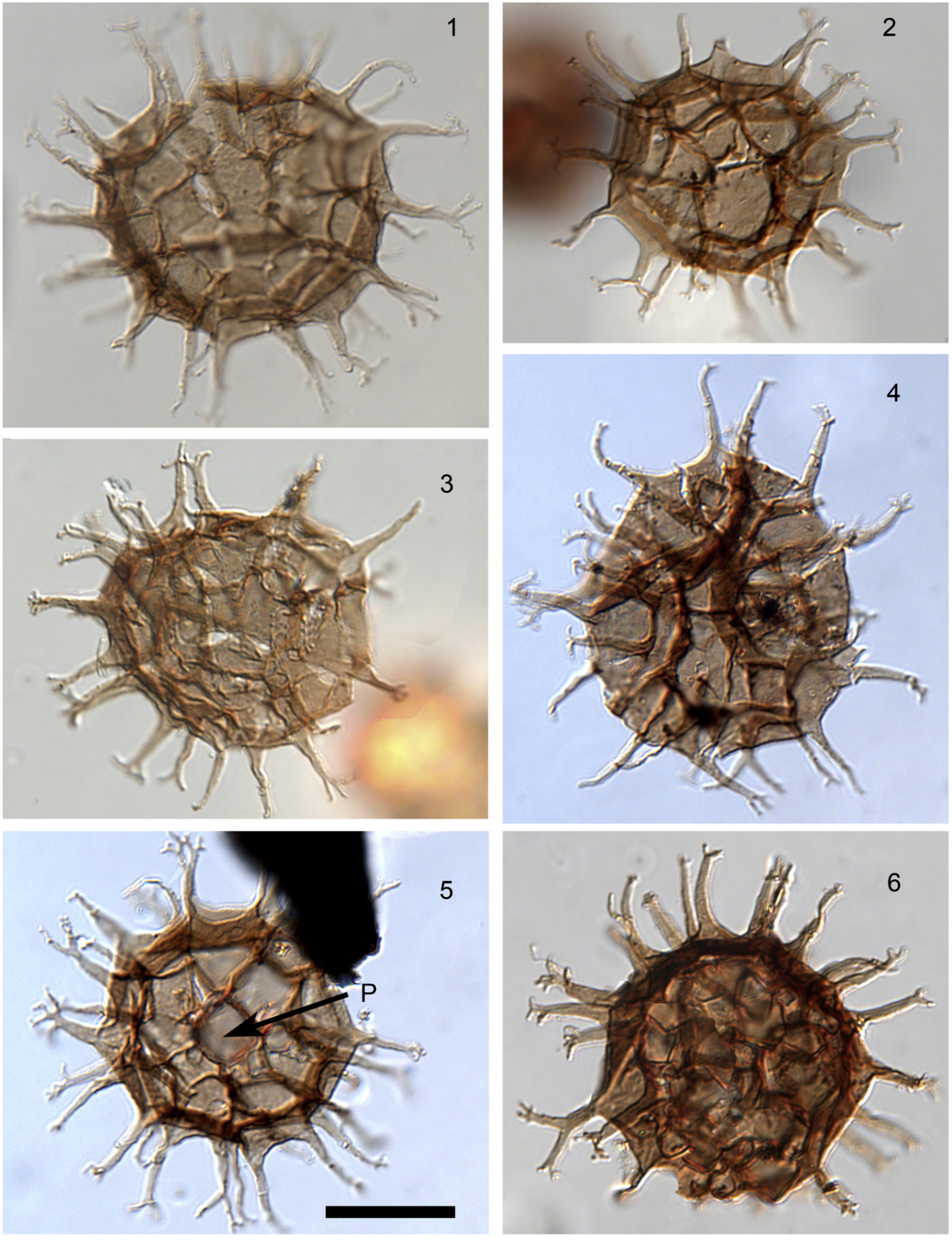
Dimensions: Vesicle width range 44–27 μm (mean 33.50 μm). Process length 7–12 μm (mean 9.43 μm), base width range 1.7–2.5 μm (mean 2.3 μm). Number of processes visible in equatorial view 27–37 (mean 31). Ratio between the length of the processes and the diameter of the vesicle 0.24–0.36 (mean 0.28). Pylome width (10–14 μm); ratio between the width of the pylome and the diameter of the vesicle (0. 33–0. 37). (Based on 70 well preserved specimens, only 4 specimens with pylome).

Discussion and comparison: Like *T. lancarae* and *T. heteromorpha* in vesicle dimensions, ornamentation, and the ratio of process length to vesicle diameter. However the number of processes is greater. The processes are homomorphic as in *T. lancarae*, however, they do not have pinnules up to fourth order.

Stratigraphic occurrence: Present record Oville Formation (Fig. 3), middle Cambrian (Drumian) IMC4–IMC5 Zone. In northern Africa (Rhadames Basin) it appears in lower levels of the Sidi-Toui Formation, assigned to the GB1 microflora, middle part of the middle Cambrian (Albani et al., 1991). In the Bourinot belt, it occurs in the MacMullin Formation (Palacios et al., 2012b).

Timofeevia heteromorpha sp. nov. (Plate XI, 1–6)

Plate XI. **(1–6)** *Timofeevia heteromorpha* sp. nov. **(1)** Holotype, OV09-11, UEXP104OV09-11-3; S-37. **(2)** OV09-11, UEXP104OV09-11-1; D-27-2. **(3)** OV09-11, UEXP104OV09-11-3; G-21-2-4. **(4)** OV09-11, UEXP104OV09-11-3; W-17-2-4. **(5)** Specimen showing a circular pylome (black arrow), OV09-11, UEXP104OV09-11-3; Z-43. **(6)** UEXP104OV09-11-2; K-39-2. Scale bar is equivalent to 20 μm.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Holotype: Sample OV09-11, UEXP104OV09-11-3, England finder coordinates S-37, Plate XI, 1.
Paratype: Sample OV09-11, UEXP104OV09-11-3, England finder coordinates Z-43, Plate XI, 5.
Type Locality: Oville section, Leon Province Fig. 1 (UTM data zone ED50 30880449, 475323352).
Type stratum: Top of alternations of mudstones and nodular limestone, bottom of the Oville Formation (Genestosa Member) (Fig. 2).
Etymology: In reference to the strongly heteromorphic processes.
Diagnosis: Spherical to polygonal vesicle with thin wall, bearing conical or distally tapering heteromorphic hollow processes, simple to ramified to the third order. The vesicle outline is polygonal or rounded and the vesicle shape grades from spherical to divided into polygonal areas (plates) limited by ridges or lines of weaknesses, usually folded, that connect the bases of the processes, located at the points of convergence of the plates. The vesicle wall is psilate to microgranulate with excystment in the form of a circular pylome.
Dimensions: Vesicle width range from 27–42 μm (mean 33.47 μm). Process length 8–12 μm (mean 10.74 μm), base width range 2–2.9 μm (mean 2.3 μm). Number of processes visible in equatorial view 20–30 (mean 24). Ratio between the length of the processes and the diameter of the vesicle 0.25–0.36 (mean 0.31). Pylome width (9–13 μm); ratio between the width of the pylome and the diameter of the vesicle (0. 28–0. 37). (Based on 59 well preserved specimens, only 5 specimens with pylome).
Dimensions of the holotype: Vesicle width 42 μm. Process length 12 μm. Base width 2.2 μm. Ratio between the length of the processes and the diameter of the vesicle 0.25.
Discussion and comparison: Similar to *T. lancarae* in vesicle dimensions and in the ratio of process length to vesicle diameter, and with which it can be confused, in particular in specimens that have lost the delicate pinnulee ornamentation. However, *T. lancarae* never has heteromorphic processes, and in *T. heteromorpha* there are no ramifications beyond the fourth order. For *T. simplex*, see below.
Stratigraphic occurrence: Oville Formation (Fig. 3), middle Cambrian (Drumian) IMC4 Zone.

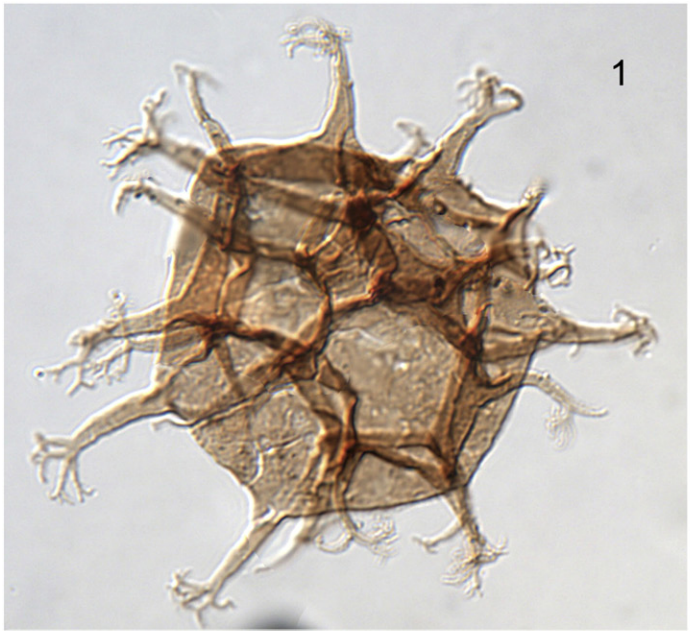
Timofeevia lancarae (Cramer and Díez, 1972) Vanguestaine, 1978 (Plate XII, 1–6).

1972 *Multiplicisphaeridium lancarae* Cramer & Díez, p. 42, Plate 1., 1–4, 6, 8
1978 *Multiplicisphaeridium lancarae* Cramer & Díez – Fombella plate. 2, 6–7
1978 *Timofeevia lancarae* (Cramer et Díez) Vanguestaine nov. comb. Vanguestaine, p. 272
1979 *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Fombella Plate 5, 70, 71, 73, 76
1981 *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Erkmen & Bozdoğan., Plate 1, 20, 21
non 1981 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Martin in Martin & Dean, Plate 6, Figs. 1–3, 8, 9, 11
1983 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Vanguestaine & Van Looy, Plate 2, 11
non 1986 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Welsch Plate 3, 18–20
1986 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Fombella, Plate 3, 19, 22
1987 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Fombella, Plate 2, 22
non 1988 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Tongiorgi in Bagnoli, Stouge & Tongiorgi, Plate 28, Fig. 9
non 1988 Timofeevia lancarae (Cramer & Díez) Vanguestaine – Martin in Martin & Dean, Plate 12, Figs. 12, 15–16
non 1989 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Hagenfeldt Plate 3, Fig. 2
1989 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Fatka, Plate II, Fig. 10
1990 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Volkova, Plate IV 6–8
1991 *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Albani et al., Plate 2, 7, 10–11
1991? *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Di Millia, Plate 2, 7, 10–11
1993 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Fombella et al., Plate II, 4
1993 *Timofeevia phosphoritica* Vanguestaine – Fombella et al., Plate 3, 5
1994 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Martin in Young et al., Fig. 12, u
1995 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Moczydłowska & Crimes, pp. 1 23–1 24, Plate 4, A–B
1997 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Martin in Dean et al., Fig. 9, f, g, m–o
1998 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Moczydłowska Fig. 46, A–B
2002 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Jankauskas, Plate 4, 1, 3; Plate 8, 1–2
2004? Timofeevia lancarae (Cramer & Díez) Vanguestaine – Brück &Vanguestaine, Plate 7, 1
2008 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Vecoli et al., Plate 1, 8, 10
non 2008 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Ghavidel-syooki & Vecoli Plate 4–6
2008 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Vanguestaine & Brück, Plate 3, 5
2009 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Palacios et al., Fig. 13. C
non 2011 *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Jachowicz-Zdanowska, Fig. 9, P
2011 *Timofeevia lancarae* (Cramer & Díez) Vanguestaine – Moczydłowska et al., Fig. 3, A–C
2012b *Timofeevia lancarae* (Cramer et Díez) Vanguestaine – Palacios et al., Fig. 9, A–B

Original diagnosis (Cramer and Díez, 1972): Central body sub-spherical, clearly differentiated from the processes. Processes radially oriented, columnar, and somewhat flexible. They are regularly bi- or tri-furcated and may bear pinnulee of up to fourth order. The processes and basal portions of some of the thickest pinnae are hollow; the remaining portions are solid. From ten to twenty processes are visible in equatorial view. The central body cavity and the process cavities are in direct, simple connection with each other.

The surface of the body and the processes is psilate. The ectoderm is about one micron thick; there is no differentiation in structure between the processes and the central body. No internal cysts or other endodermal structures. The mode of opening of the ectoderm is not known.
Description: Spherical to polygonal vesicle with thin wall, bearing conical or tapering regular hollow processes, freely, connecting with the cavity of the vesicle. Process ramified up to the third order ending in solid fine hair-like pinnules up to fourth order. Vesicle shape grades from spherical to divided into polygonal areas (plates) limited by ridges or lines of weaknesses, usually folded, that connect to the bases of the

Plate XII. **(1–6)** *Timofeevia lancarae* (Cramer & Díez, 1 972) Vanguestaine, 1978 **(1, 3, 4)** Polygonal vesicle partially subdivided into polygonal plates, delimited by folded areas that connect to the bases of the processes. **(1)** AD06-2, UEXP104AD06-2-1; J-38-1. **(3)** AD06-2, UEXP104AD06-2-1; C-34. **(4)** UEXP104AD06-2-1; F-41-1. **(2)** Specimen showing a circular pylome (black arrow), AD06-2, UEXP104AD06-2-1; T-17-1. **(5)** Specimen showing the aspect of fine hair like pinnule with up to four orders of branches, AD06-2, UEXP104AD06-2-1; L-14. **(6)** Flattened spherical vesicle showing a circular pylome (black arrow) AD06-2, UEXP104AD06-2-2; P-24. Scale bar is equivalent to 20 μm.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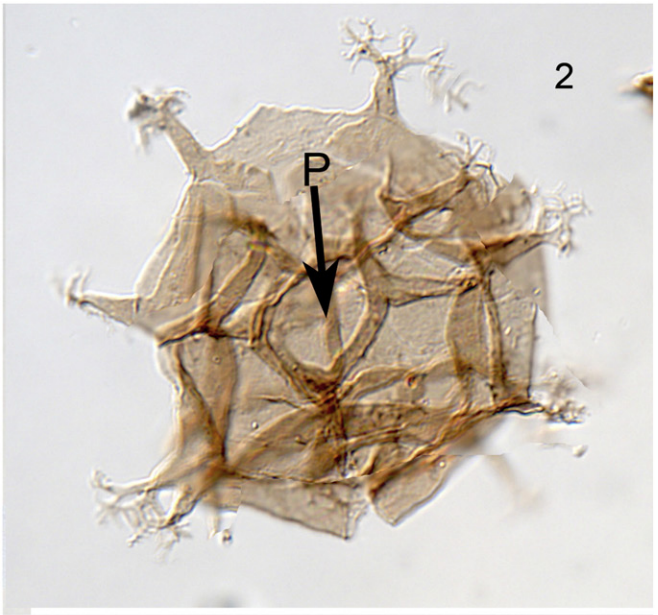
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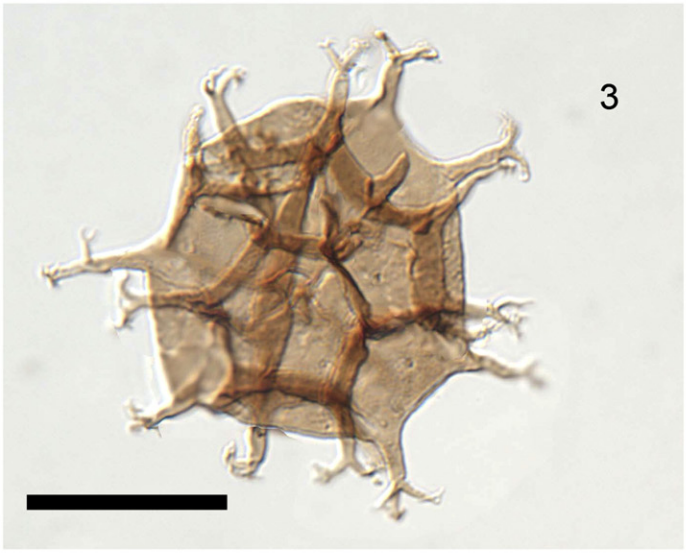
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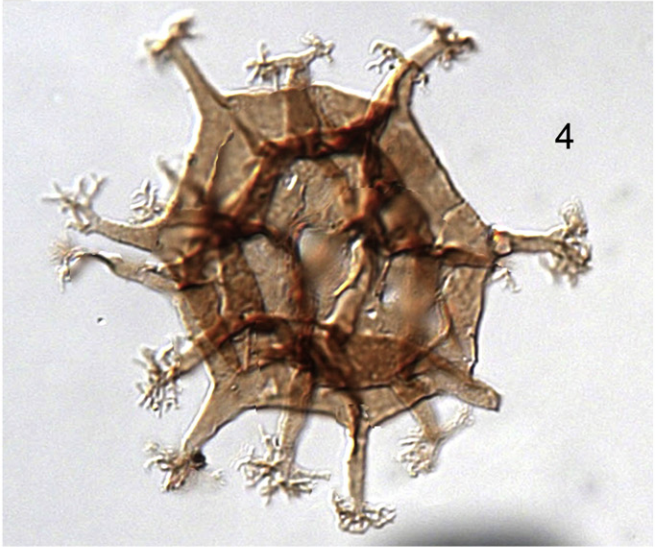
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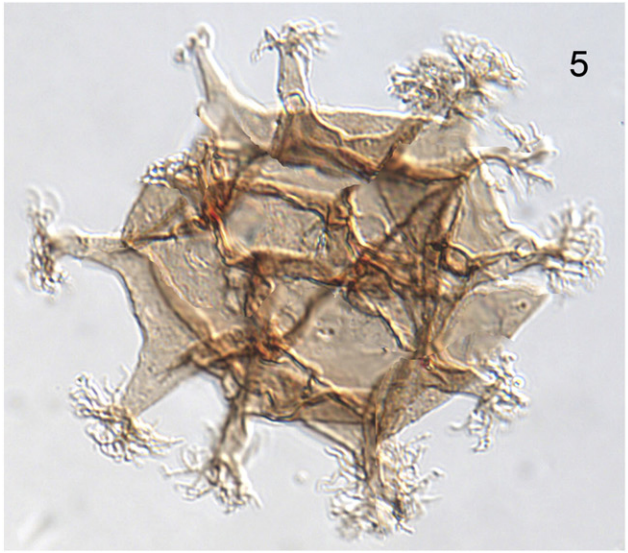
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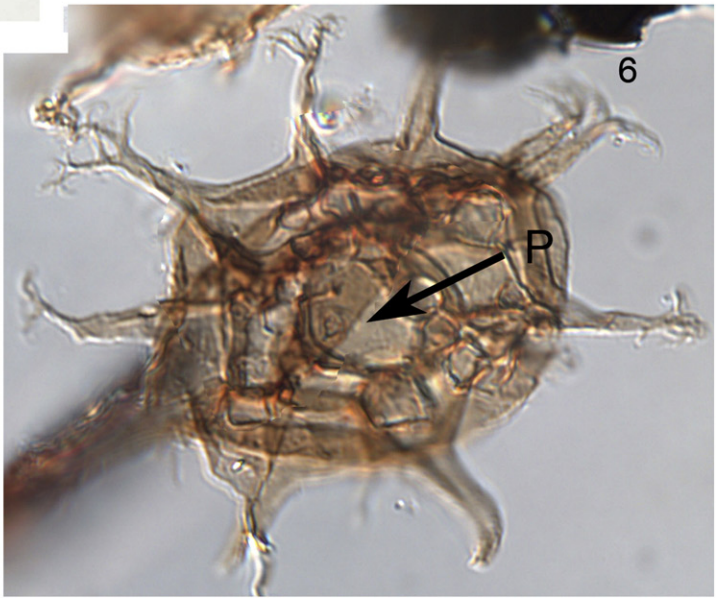
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processes, which are located at the points of convergence of the plates. The vesicle wall is psilate and rarely microgranulate, with excystment in the form of a circular pylome.

Dimensions: Vesicle width 24–48 μm (mean 34 μm). Process: length 7–14 μm (mean 10.5 μm), base width 1.6–4.5 μm (mean 2.9 μm). Number of processes 10–21 (mean 15). Ratio between the length of the processes and the diameter of the vesicle 0.23–0.38 (mean 0.29). Pylome width (10–15 μm). ratio between the width of the pylome and the diameter of the vesicle (0. 33–0. 37). (Based on 264 well preserved specimens; only 11 specimens with pylome).

Discussion and comparison: Vanguestaine (1978), believes that the polygonal contour is dependent on the number of plates. Here, it is considered that the contour probably depends on the development of the cyst. Specimens with the same number of processes and plates present an indistinctly spherical (Plate XII, 5–6) or polygonal (Plate XII, 1–4) outline. The tapering processes are hollow, mainly rigid, radially arranged, and regularly branched to the third order, ending in solid fine hair-like pinnules that are ramified up to the fourth order (Plate XII, 4–6). The delicate pinnules are easily lost (Plate XII, 1, 3). The number of processes ranges between 10 and 21, in accordance with Cramer and Díez (1972)'s description of *M. lancarae*.

The presence of a circular pylome and incipient plates, are characters observed in other Drumian species, such as *Cristallinium cambriense* (Pl. II, 3; see also Moczydłowska et al., 2011, Fig. 3 D, E) and *Vulcanisphaera cantabrica* sp. nov. (Pl. XV, 4).

Other similar species, such as *Stelliferidium albani* and *Stelliferidium magnum*, differs from *Timofeevia lancarae* by their heptagonal pylome, radiating striations, and cylindrical and flexible processes with conical bases (Palacios et al., 2009).

Stratigraphic occurrence: Oville and Barrios Formations, middle Cambrian (Drumian-Guzhangian, IMC4–IMC6 Zones, Fig. 3). middle Cambrian, Playón Formation, southern Spain *Solenopleuropsis* and post-*Solenopleuropsis* beds (Palacios, 2008; Moczydłowska et al., 2011). middle Cambrian, Morocco (Vanguestaine and Van Looy, 1983); middle-upper Cambrian, western Libya–southern Tunisia (Albani et al.1991) and northwestern Algeria (Vecoli et al., 2008). middle Cambrian, southern Turkey top of the Koruk Formation and the Sosink Formation *Solenopleuropsis* and post-*Solenopleuropsis* interval (Erkmen and Bozdogan, 1981; Dean et al., 1997). Czech Republic, middle Cambrian Jince Formation, *Onymagnostus hybridus* Zone (Fatka, 1989). Southeastern Ireland, Booley Bay Formation, middle-Upper Cambrian (Moczydłowska and Crimes, 1995; Vanguestaine and Brück, 2008). Northwestern Wales, Upper Cambrian (Martin's A2 and A3 zones), Maentwrog and Ffestiniog Formations (Young et al., 1994). Southeastern Cape Breton Island, Nova Scotia, in Canada: Mira River area, MacLean Brook Formation (middle Cambrian (*P. davidis* Zone) to lower Furongian (Palacios et al., 2009) and Bourinot Belt, MacMullin Formation (Palacios et al., 2012b). Poland, Upper Silesia, Sosnowiec Formation, middle Cambrian, *P. paradoxissimus* Super Zone, and Jaszczurowa Formation Upper Cambrian (Moczydłowska, 1998). East European platform, Lithuania, Panierai Formation (*Paradoxides paradoxissimus* Zone) (Jankauskas, 2002) and SK2 Horizon (*P. paradoxissimus* and *P. forchhammeri* zones) (Volkova, 1990; Volkova and Kiryanov, 1995). Southeastern Cape Breton Island, Nova Scotia, in Canada: Mira River area, MacLean Brook Formation (middle Cambrian (*P. davidis* Zone) to lower Furongian (Palacios et al., 2009) and Bourinot Belt, MacMullin Formation (Palacios et al., 2012b).

Timofeevia simplex sp. nov. (Plate XIII, 1–4)

Holotype: Sample OV06-4, UEXP104OV06-4nn2, England finder coordinates W-18, Plate XIII, 1.

Type Locality: Oville section, SE Oville village, Leon Province Fig. 1, 3 (UTM data zone ED50 30880449, 475323352).

Type stratum: Genestosa Member, Oville Formation, in alternations of mudstones and nodular limestone (Fig. 3).

Etymology: Latin, *simplex*, with reference to simple processes.

Diagnosis: Polygonal to rarely spherical vesicle with thin wall, bearing conical or distally tapering simple hollow processes, distally pointed. The vesicle is divided into polygonal areas (plates) that connect the bases of the processes, located at the points of convergence of the plates. The vesicle wall is psilate.

Dimensions: Vesicle width range 25–52 μm (mean 35 μm). Process length 7–15 μm (mean 11.3 μm), base width range 1.5–3 μm (mean 2.1 μm). Number of processes visible in equatorial view 21–30 (mean 25.4). Ratio between the length of the processes and the diameter of the vesicle 0.25–0.37 (mean 0.32). (Based on 63 well preserved specimens.)

Dimensions of holotype: Vesicle 40 μm. Process length 10 μm, base width 2.5 μm. Number of processes 20. Ratio between the length of the processes and the diameter of the vesicle 0.25.

Discussion and comparison: Sporadically some specimens have 1 or 2 bifurcate processes and the distal part of the processes is flexible. Vesicle divided into pentagonal and hexagonal plates limited by ridges or lines of weaknesses that are usually folded, connecting the bases of the processes, located at the points of convergence of the plates. Some specimens seem to have a circular pylome (Pl. 13, 2), although this is unclear. *T. simplex* includes the oldest *Timofeevia* in the fossil record.

The dimensions and number of processes are similar to those of *T. heteromorpha* sp. nov., with the fundamental difference being in the type of processes. Possibly, there is a gradual transition between *T. simplex* and *T. heteromorpha* sp. nov.

Stratigraphic occurrence: Oville Formation (Fig. 3) middle Cambrian (Drumian) IMC3, and lower IMC4 Zone.

Genus ***Tubulosphaera*** Palacios 1998

Type species: *Tubulosphaera perfecta* Palacios 1998.

Tubulosphaera craterae sp. nov. (Plate XIV, 1–4)

1987 *Lophodiacrodium vozmedianum* Fombella sp. nov. — Plate 1, 15

2012b *Tubulosphaera* sp. Palacios et al., Fig. 10, C

Holotype: Sample AD06-18, UEXP104AD06-18-1, England finder coordinates O-26-4, Plate XIV, 1.

Paratype: Sample AD06-11, UEXP104AD06-11-1, England finder coordinates O-26-4, Plate XIV, 4.

Type Locality: Adrados section, Oville Formation, Leon Province Fig. 1 (UTM data zone ED50 31448376, 474923731).

Type stratum: Oville Formation, Alternations of sandstone and glauconitic siltstone-mudstone, Adrados Member of the Oville Formation.

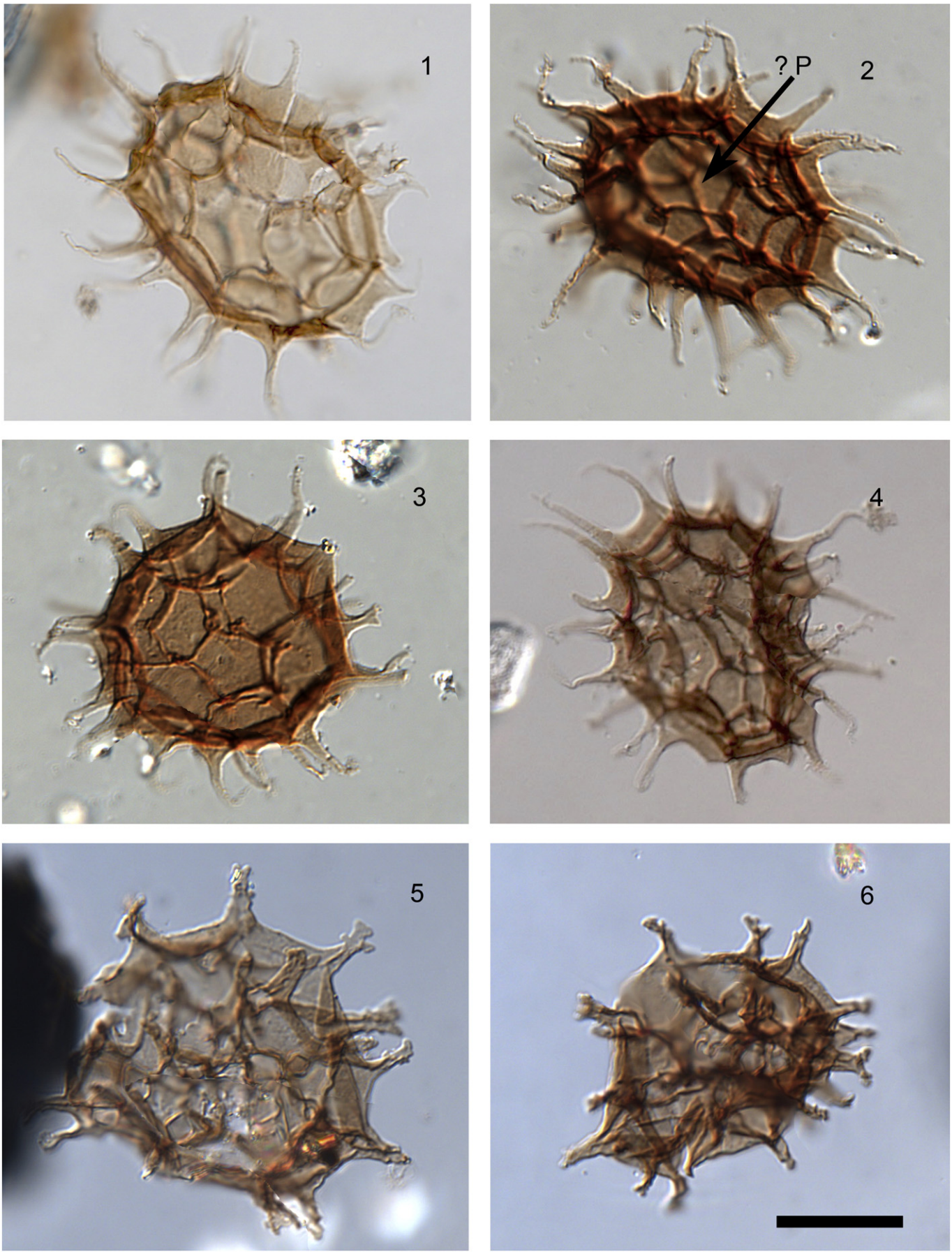
Etymology: From Latin *crater* (crater), for the crater-like appearance of depressions on the surface of the vesicle.

Diagnosis: Spherical to ellipsoidal vesicle with wall of variable thickness, bearing numerous short tubular processes freely connected with the vesicle's interior and irregularly arranged. The process terminations are flat or slightly convex. The processes are easily lost, leaving only the ring-shaped basal part, which gives the surface of the vesicle a crateriform aspect. Excystment by median split.

Dimensions: Vesicle width 28–88 μm (mean 48 μm). Process length 2–3 μm (mean 2.3 μm). Process width 1.5–3 μm. (mean 2.30 μm). Number of processes in visible area 13–69 (mean 30). (Based on 43 specimens.)

Discussion and *comparison*: Specimens of *T. craterae* with median split have been classified erroneously as diacrodians (*Lophodiacrodium vozmedianum*, Fombella, 1987). The species differs from *Tubulosphaera perfecta* by having shorter, irregularly distributed, processes, and the

Plate XIII. **(1–4)** *Timofeevia simplex* sp. nov., specimens showing polygonal and hexagonal plates. **(1)** Holotype, OV06-4, UEXP104OV06-4nn2-W-19. **(2)** Specimen showing probable circular pylome (black arrow), OV09-8, UEXP104OV09-8-2; F-27. **(3)** OV09-8, UEXP104OV09-8-3; F-22-4. **(4)** OV06-3, UEXP104OV06-3 N; X-36. **(5–6)** *Timofeevia raquelinae* (Cramer and Díez) Cramer and Díez, 1979, specimens showing typical manate processes. **(5)** OV09-11, UEXP104OV09-11-3; T-38. **(6)** OV09-11, UEXP104OV09-11-3; Z-16-3. Scale bar is equivalent to 20 μm.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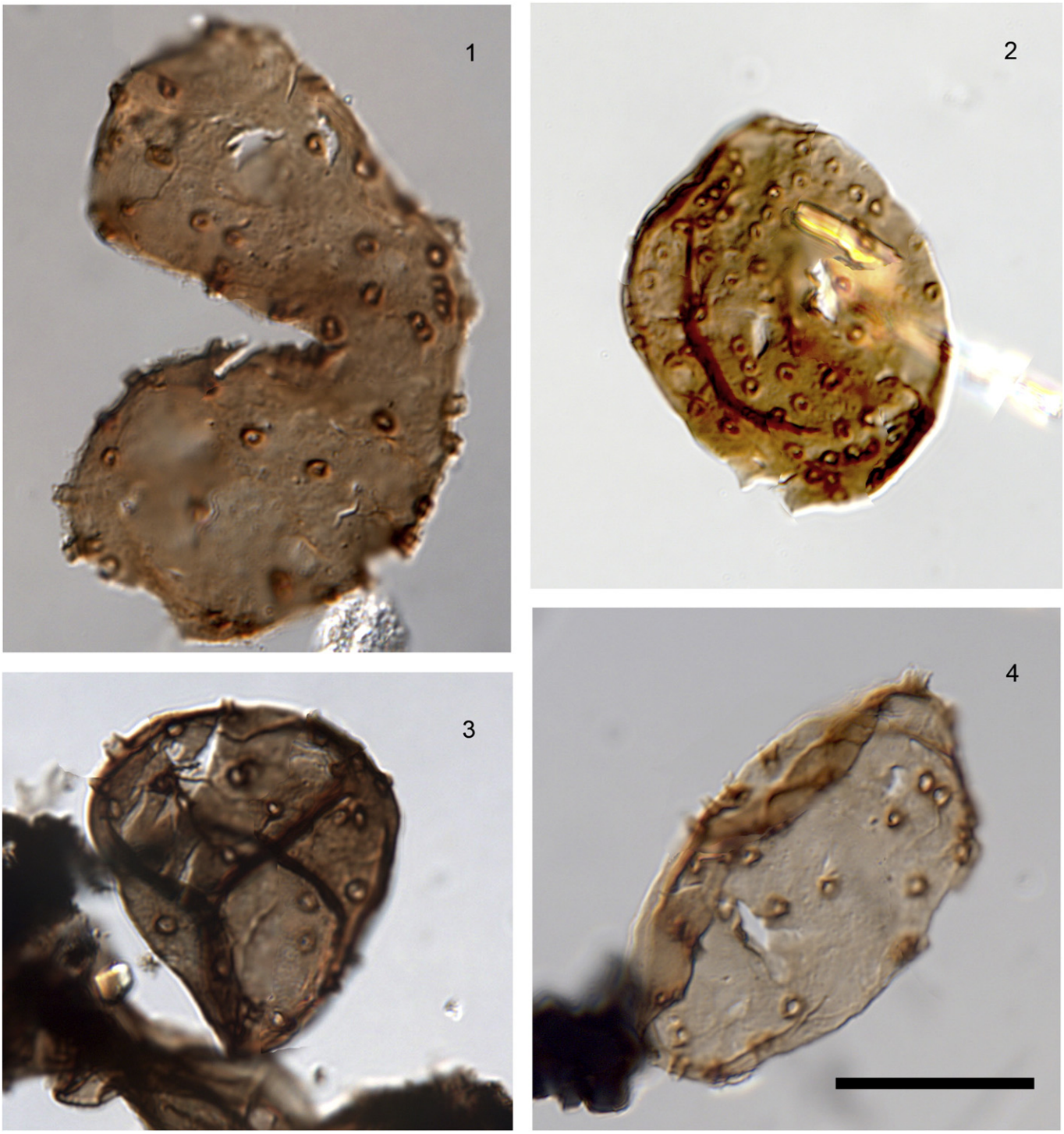


Plate XIV. (**1–4**) *Tubulosphaera craterae* sp. nov. (**1**) Holotype, AD06-18, UEXP104AD06-18-1; O-26-4. (**2**) AD06-11, UEXP104AD06-11-2; D-42-3. (**3**) BL06-6, UEXP102BL06-6-2; E-36. (**4**) AD06-6, UEXP104AD06-6-2; O-27-1-2. Scale bar is equivalent to 20 μm.

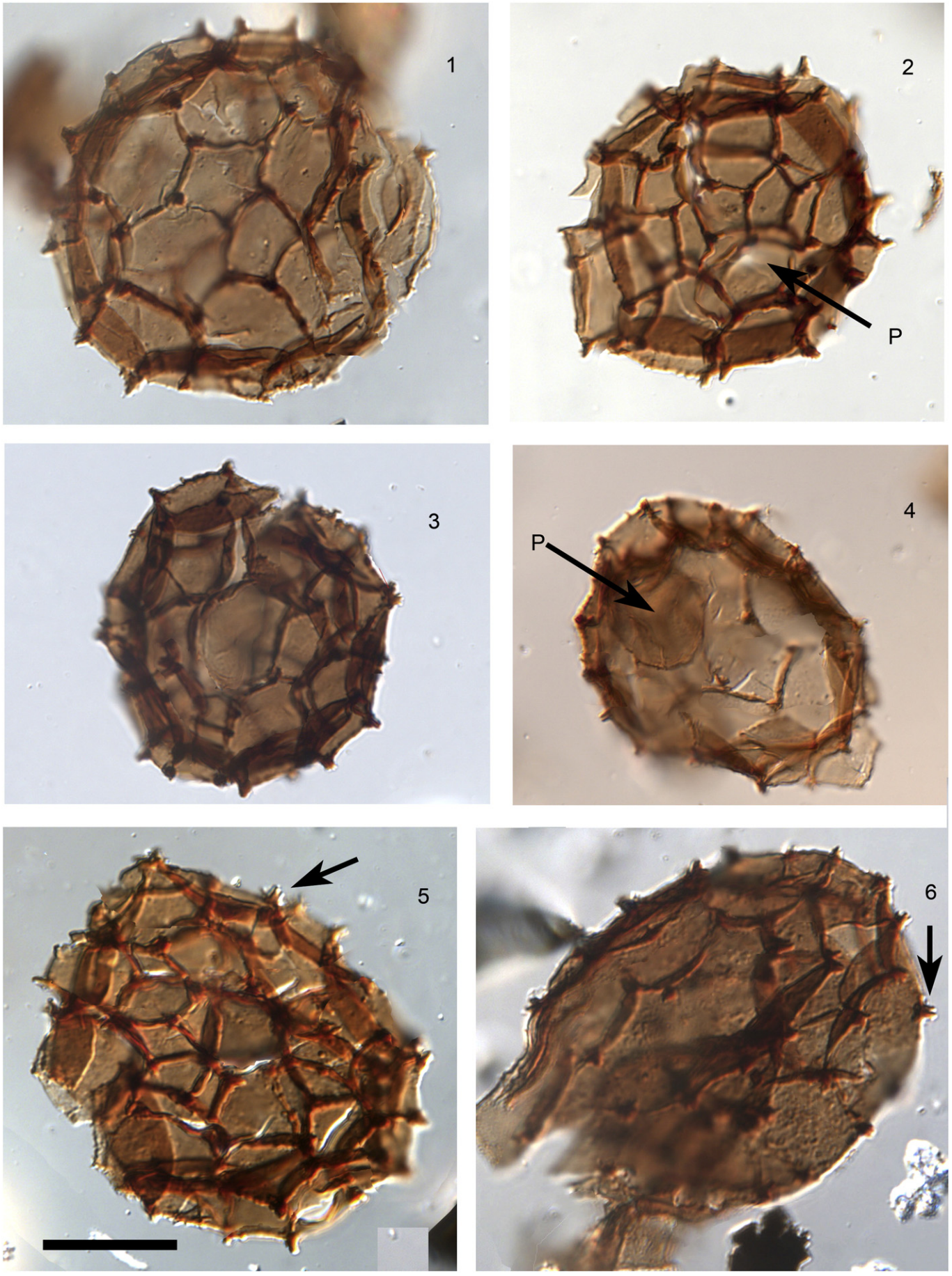
processes frequently break, leaving only a basal ring. There is a greater variability in vesicle diameter than seen in *T. perfecta*, which also lacks any evidence of excystment by median split.

Stratigraphic occurrence: Present record, Oville Formation, and lower part of the Barrios Formation, Upper Drumian–Guzhangian (Languedocian) and the MacMullin Formation Bourinot Belt, Cape Breton Island, Canada, Upper Drumian–Guzhangian (Palacios et al., 2012b).

Genus ***Vulcanisphaera*** Deunff, 1961 emend. Rasul, 1976

Type species: *Vulcanisphaera africana* Deunff, 1961 by original designation.

Plate XV. (**1–6**) *Vulcanisphaera cantabrica* sp. nov. (**1**) Holotype, OV09-6, UEXP104OV09-6-2; G-38-4. (**2**) Specimen showing circular pylome (black arrow), OV09-6, UEXP104OV09-6-1; E-27. (**3**) OV09-6. UEXP104OV09-6-2; E-36-3. (**4**) Paratype, specimen showing circular pylome (black arrow), OV09-6, UEXP104OV09-6-1; M-28-2. (**5, 6**) Specimens showing short trifurcated processes (black arrow). (**5**) OV09-6, UEXP104OV09-6-2; P-44-1-2. (**6**) OV06-2a, UEXP104OV06-2a-1; U-21-1. Scale bar is equivalent to 20 μm.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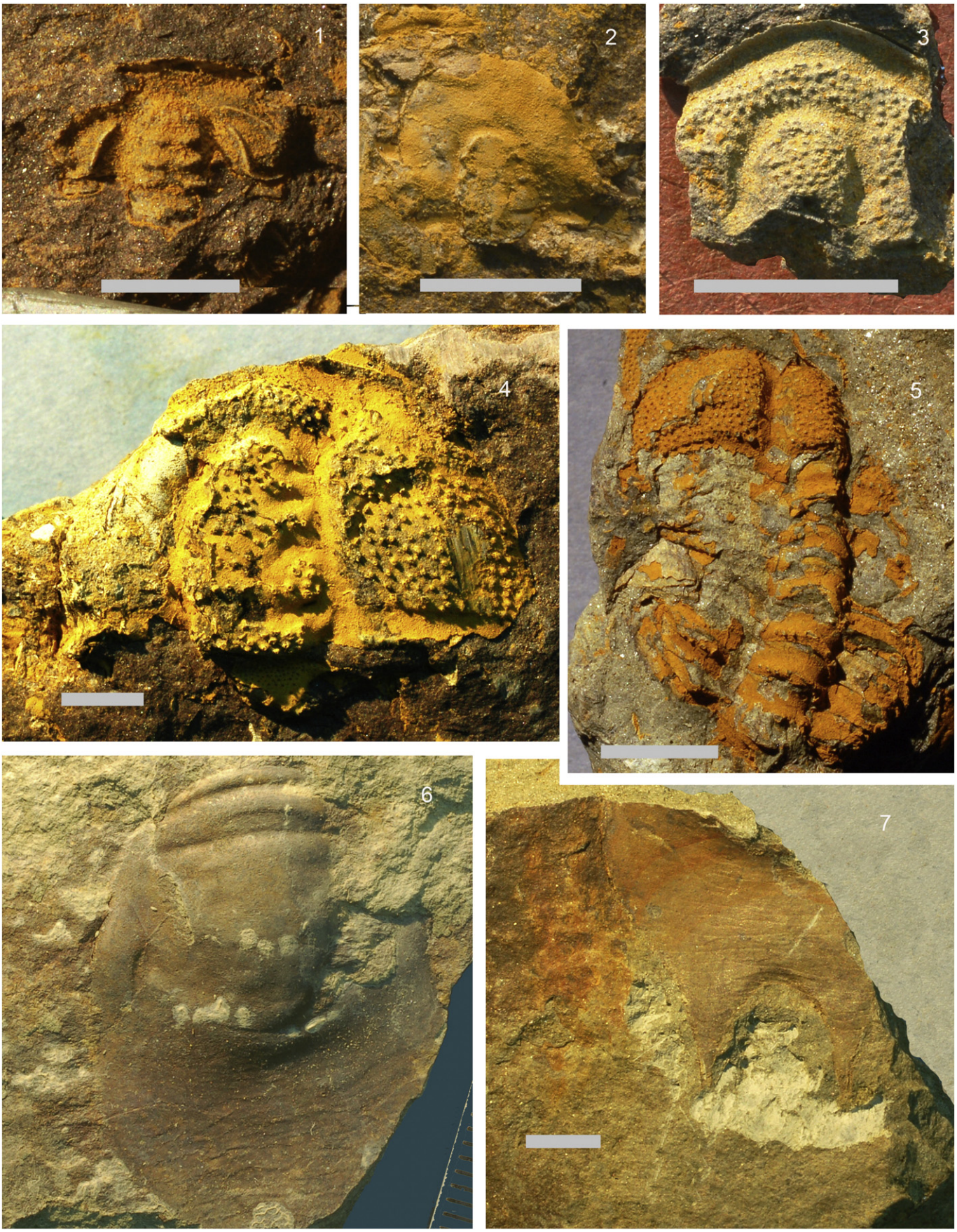

Plate XVI. Trilobites from the Oville Formation in Adrados and Oville sections. Scale bar **(2)** 2.5 mm and **(2–7)** 5 mm. **(1)** *Badulesia granierii* OV06T1. **(2)** *Agraulos* sp. OVT1. **(3)** *Solenopleuropsis* sp. OVT2. **(4)** *Parabailiella*? sp. OVT1. **(5)** *Solenopleuropsis* sp. ADT-1. **(6, 7)** *Paradoxides brachyrhachis* ADT-2.

Vulcanisphaera cantabrica sp. nov. (Pl. XV, 1–6)

2006 *Vulcanisphaera lanugo* Martin in Martin & Dean – Palacios et al. (mentioned in text)

2008 *Vulcanisphaera lanugo* Martin in Martin & Dean – Palacios Fig. 3, D.

2012 *Vulcanisphaera lanugo* Martin in Martin & Dean – Palacios et al., Fig. 6, C

Holotype: Sample OV09-6, UEXP104OV09-2, England finder coordinates G-38-4, Plate XV, 1.

Paratype: Specimen showing circular pylome, OV09-6, UEXP104OV09-6-1; M-28-2., Plate XV, 4.

Type Locality: Oville section, Oville Formation, Leon Province Fig. 1 (UTM data zone ED50 314805, 4749311).

Type stratum: Oville Formation, alternations of mudstones and nodular limestone, bottom of Oville Formation (Genestosa Member) (Figs. 1, 2, 4).

Etymology: Cantabrica, from Cantabrian Mountains.

Diagnosis: Vesicle polygonal in outline, thick wall with psilate to rarely granulate surface. Vesicle divided into 18 to 23 polygonal plates (mainly pentagonal and hexagonal). The suture zones of the plates are frequently ornamented with small solid spines unevenly distributed. Very short conical solid processes limited to the points of union of the plates. Distal terminations of processes mainly simple, rarely bifurcated or trifurcated. Excystment in the form of a circular pylome.

Dimensions: Vesicle width 37–60 μm (mean 50.7 μm). Conical process length 1. 5–2. 5 μm (mean 2. 3 μm). Number of plates in visible area 18–23 (mean 20). Pylome (only five specimens), width (15–17 μm) and ratio between diameter pylome and vesicle (0.31–0.33). (Based on 57 well preserved specimens.)

Discussion: Vesicle wall breaks easily along the sutures of the polygonal plates (Plate XV, 4). *Vulcanisphaera lanugo* Martin in Martin and Dean (1988) is very similar to *V. cantabrica*, but its size is much smaller (not exceeding 35 μm), its wall thinner, and it has long and delicate processes that are easily lost. Specimens of *V. lanugo* that have lost the processes are very similar to *V. cantabrica*. Also not previously observed in *Vulcanisphaera* is the presence of a circular pylome (Plate XV, 4), character of diagnostic significance also observed in *Timofeevia* and *Cristallinium* (see above). Specimens with ornamented suture lines are similar to *Cristallinium cambriense*, but without processes on the intercession of the plates, and ornamentation evenly distributed.

Stratigraphic occurrence: Present record in the Genestosa Member, lower part of the Oville Formation (ICM2 Zone). Lower part of the Playón Formation in southern Spain (Palacios et al., 2006). In Nova Scotia's Bourinot belt, it occurs in the upper part of the lower Drumian Dugald Formation.

6. Conclusions

The presence of a continuous record of acritarchs in the Oville Formation allows the recognition of a detailed biozonation of Cambrian Series 3 (Fig. 8), and its correlation with Baltica and Avalonia (Fig. 9).

The IMC1 Zone is well represented in southern Spain (Palacios et al., 2006), and corresponds approximately to the regional Leonian Stage, equivalent to Stage 5. Its lower limit is well defined in southern Spain, although it is not calibrated by the presence of trilobites.

The lower limit of the IMC2 Zone, equivalent to the base of the *Badulesia tenera* Zone, coincides approximately with the base of the Drumian. The IMC2–IMC4 Zones are well calibrated by the presence of trilobites, and correspond to the Caesaraugustian (Figs. 8, 9).

The lower limit of the IMC5 Zone is calibrated by the presence of lower Languedocian trilobites. No trilobites are known within the IMC6 Zone, although the correlatable lower A2 Zone in Newfoundland is equivalent to the *P. forchhammeri* Zone. Both zones have been included in the Languedocian.

The base of the Oville Formation is traditionally considered to be diachronic. Here, it is considered probable that this diachronism has been magnified by the presence of mechanical contacts between the Oville and Láncara Formations, suggesting that the scale of the diachroneity needs reconsideration.

The possibility of establishing detailed acritarch biozones in the Cambrian, together with the cosmopolitan nature of the acritarchs and the apparent absence of provincialism in the middle Cambrian, reinforces its value for Cambrian chronostratigraphy, its importance for establishing detailed correlations between Gondwana, Baltica, and Avalonia, and its great potential for the establishment of a common chronostratigraphic scale valid for Avalonia, Baltica, and northwestern Gondwana.

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